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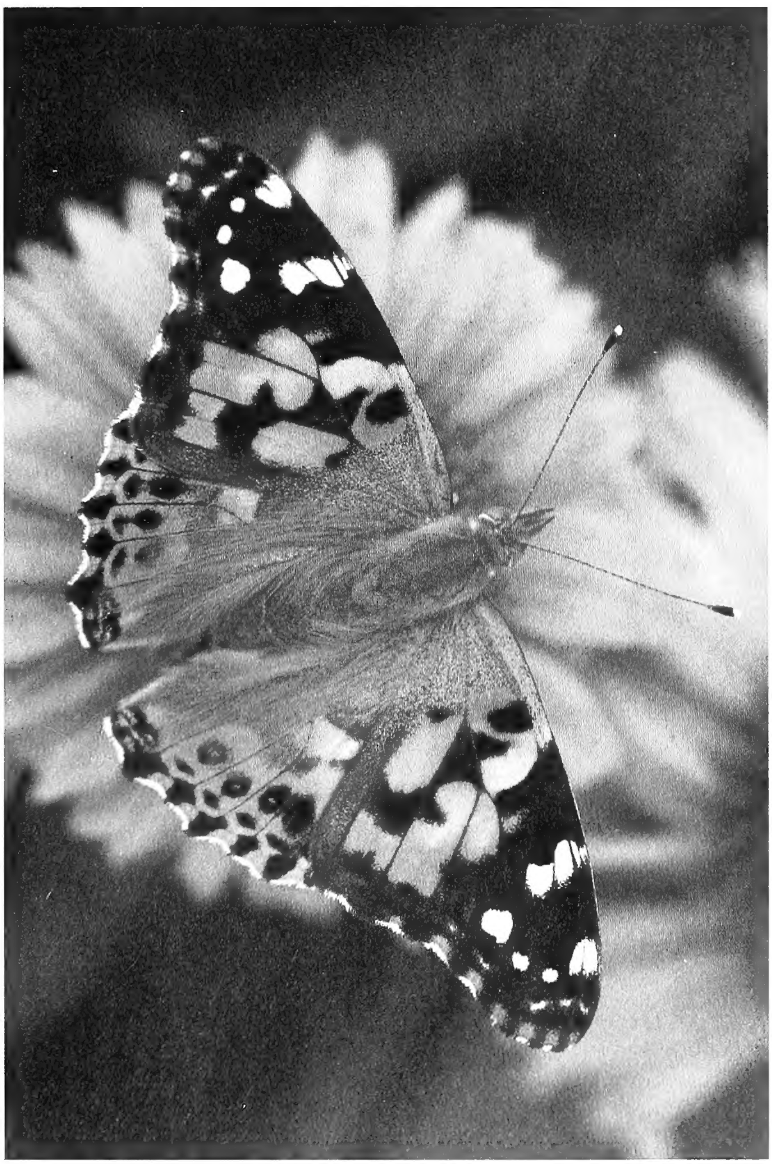

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PAPILIONOIDEA OF THE EVERGREEN TROPICAL FORESTS OF MEXICO

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ABSTRACT. The diurnal butterflies in 11 geographical units of evergreen tropical forest in Mexico were studied, giving in a total list of 683 species of Papilionoidea (excluding Hesperiidae). This is the first list of Mexican butterflies which covers a specific type of vegetation. The species richness in this zone makes evident the need for adequate conservation strategies for these ecosystems, whose extent is rapidly decreasing. The results are compared with other areas of Neotropical rain forest.

Additional key words: butterflies, distribution, evergreen tropical forest, Neotropical region, richness.

RESUMEN. Se efectuó un trabajo de mariposas diurnas en 11 unidades geográficas con bosque tropical perennifolio en México, registrándose una lista total de 683 especies de Papilionoidea (sin incluir Hesperiidae). Ésta es la primera lista de mariposas en México que involucra la cobertura de un tipo de vegetación específico. La riqueza de especies presentes en la zona hace patente la necesidad de crear estrategias de conservación en este ecosistema que está disminuyendo su extensión rápidamente. Los resultados se comparan con otros sitios de bosque tropical del Neotrópico.

Palabras claves: mariposas, distribución, bosque tropical perennifolio, región Neotropical, riqueza.

The rain forests, or evergreen tropical forest (ETF) ecosystems are considered top priority for world conservation. This is because these forests shelter approximately 50% of the species of the planet Earth. In addition, their rate of decrease is one of the fastest (Wilson 1988, Dirzo & García 1992). The Neotropical region contains approximately 20% of the species on the Earth (Myers 1988); within this region, the ETF has the largest extent of all the regions.

The northernmost distribution of the ETF in America is in México. Originally, the ETF covered 13% of the nation, but Granillo (1985) and Toledo (1988) remark that at present it covers from 10 to a 15% of the original area, being replaced by pastures and other agroecosystems. An annual deforestation rate of 4% was registered for the last 25 years by Dirzo & García (1992) in the ETF of the Los Tuxtlas region in Veracruz, México.

The ETF was once distributed in México from southern San Luis Potosí and northern Veracruz, in the north, through parts of the states of Hidalgo, Puebla, Oaxaca, southern Veracruz, to the north and northeast of Chiapas and in some parts of Tabasco, Campeche and Quintana Roo (Fig. 1). Along the Pacific slope, it occupied the southernmost area of Sierra Madre de Chiapas and the Tapachula-Mapastepec (low Soconusco region), isolated by the Sierra Madre, the Tehuantepec isthmus and the Central Depression of Chiapas (Rzedowski 1978). Rzedowski (1996) estimated that the plant species in the ETF include over a third of the total flora of the country.

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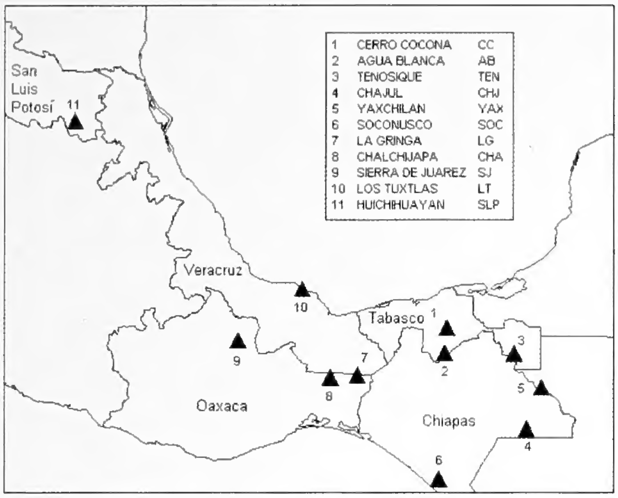

FIG. 1. Distribution in México of the geographical units having evergreen tropical forests.

Although Papilionoidea have been the subject of many studies, the knowledge of this lepidopteran superfamily is still very incomplete. Robbins & Opler (1997) estimated its approximate richness as 17,500 species; furthermore, they pointed out that this is one of the most studied groups of insects, with 90% of its species being known. These authors assumed that the greatest richness of this group is within the Neotropical region; similar results were obtained by Heppner (1991). There are not enough faunistic studies in the region and many of the studies were based on sporadic collections in extensive, ecologically heterogeneous areas. The situation becomes more critical in the ETF, whose understanding is based on very few studies, most of which were made during this century in a few areas, such as Los Tuxtlas, Veracruz and Sierra de Juárez, Oaxaca in México.

The studies made by Lamas et al. (1991, 1996), Brown (1984), Emmel & Austin (1990), and Austin et al. (1996), among others, show the need for making more intensive systematic collections in these communities, especially in areas located close to mountains (increasing the diversity; G. Lamas pers. com.). Because of the inaccessibility of the areas occupied by the ETF and the consequent logistic and financial problems for systematic studies there, methods have been proposed to estimate the potential number of species living in each community in a quick and accurate way (Soberón & Llorente 1993, Colwell & Coddington 1994).

The large diversity of butterflies living in the ETF of México has attracted attention of interested students since the 19th century; nevertheless, only about 10 faunistic studies are available which can be compared with some accuracy, such as those made by Hoffmann (1933), Ross (1964, 1976-1977), Routledge (1977), de la Maza & de la Maza (1985a, b), de la Maza & White (1990), Luis et al. (1991, 1995), Raguso & Llorente (1991, 1997), Martínez (1994), and Villegas (1998).

MATERIALS AND METHODS

The first step to obtain a list of the butterflies species inhabiting the ETF in México was to compile, systematize and summarize the studies made in these communities. A specialized bibliography was consulted for five states: Tabasco, Routledge (1977), Martínez (1994) and Villegas (1998); Chiapas, Hoffmann (1933), de la Maza & de la Maza (1985a, 1985b), and unpublished data of faunistic surveys made in Yaxchilán by members of the Museo de Zoología de la Facultad de Ciencias, UNAM; Oaxaca, the data available for the Chimalapas region and Luis et al. (1991); Veracruz, Ross (1964, 1976-1977), Raguso & Llorente (1991, 1997) and Luis et al. (1995); for San Luis Potosí, de la Maza & White (1990). The bibliography was used to obtain comparable lists, in order to be able to tabulate the data by region and by locality. Only records with vouchers collected in ETF were considered.

Once the areas in each report were analyzed, "geographical units" were defined for each collection site, giving 11 units (Fig. 1): in Tabasco, Cerro del Coconá (CC), Agua Blanca (AB) and Tenosique (TEN); in Chiapas, Chajul (CHJ), Yaxchilán (YAX) and Soconusco (SOC); in Oaxaca, La Gringa (LG), Chalchijapa (CHA) and Sierra de Juárez (SJ); in Veracruz, Los Tuxtlas (LT); and in San Luis Potosí, Huichihuayán (SLP).

For the geographical units LT, SJ and SLP, only the localities having ETF were included, since the original studies were made in several plant communities. As these studies included sites whose altitudes do not correspond to the distribution of the ETF, a detailed revision was made so as not to overestimate the richness of the fauna by inclusion of montane species or those of semideciduous tropical forest.

RESULTS AND DISCUSSION

Based on the above defined 11 units, 683 species living in the ETF of México were registered, in 272 genera, 18 subfamilies and 4 families, about 53% of the total butterfly fauna of the country (assuming a total of 1,295 species of Papilionoidea and excluding the Hesperiidae). The percentage of species in each family is similar to that reported in other regions of México (Sierra de Manantlán, Jalisco-Colima: Vargas et al. 1999;

Sierra de Atoyac de Álvarez, Guerrero: Vargas et al. 1992): Papilionidae 5.4%, Pieridae 7.7%, Nymphalidae 45.1%, and Lycaenidae 41.7%.

Even though the studies chosen for this analysis used different methods, time periods and objectives, a general comparison is presented for each of the 11 geographical units by species in each family and subfamily, together with the estimated total number of species inhabiting the ETF in México (Table 1).

According to Llorente et al. (1993) and Luis et al. (2000) the butterfly fauna of México represents about 10% of the wold total, thus indicating that México is a megadiversity country. In this paper only a single plant community was analyzed, covering 13% of the total land surface; due to deforestation over the last 50 years, this is now reduced to less than 2%. The percentage of species living in this plant community is surprisingly high, representing 50% of the Mexican butterfly fauna. Heppner (1991) gave a total of 7,927 species of butterflies in the Neotropical region, including the family Hesperiidae, which was excluded in the present paper; even so the ETF included 8.6% of this fauna. If only the 4,800 species of Papilionoidea are considered, the ETF in México holds 14.2% of this figure.

Table 1 also includes the percentage of the Mexican total in each subfamily. This table shows that LT is the most diverse geographical unit, with 482 species (70.6%), followed by SJ with 355 (52%), CHJ with 352 (51.5%), and SLP with 300 (43.9%). The latter geographical unit is the northernmost ETF site in México, followed by LT and SJ. Considering that México is in a transitional biogeographical zone between the Nearctic and the Neotropical regions, and that the predominance of these elements varies with latitude and altitude, this suggest an increase of species with clear Nearctic affinity, which do not belong to the ETF in a strict sense.

The geographical units LT, SJ and CHJ have similar patterns of number of species per subfamily, with the exception of the Theclinae in LT, which include 54.78% of the species mentioned for ETF, or 50% of those for all of México. This may be due to the fact that, for many years, amateur collectors have paid local people for hairstreak specimens (L. González-Cota pers. com.). This collecting effort is clearly seen in the percent representation (Table 1).

The geographical unit LT has the highest representation for 8 out of 18 subfamilies collected. Heppner (1991) mentioned the importance of the Ithomiinae, Morphinae and Brassolinae, which have maximum number of species in the following geographical units: Ithomiinae in SJ with 21 species; Morphinae in CHJ, CHA, SJ and LT with three species; and Brassolinae in CHJ and LT with 11 species.

TABLE 1. Species richness of Papilionoidea by geographical unit. See 'Methods' for abbreviations.

	CC	AB	TEN	CHJ	YAX	SOC	LG	CHA	SJ	LT	SLP	ETF	MEX
Papilionidae	**6**	**5**	**7**	**9**	**8**	**4**	**8**	**5**	**11**	**10**	**9**	**12**	
Papilioninae	15(18.29)	11(13.41)	14(17.07)	24(29.27)	15(18.29)	9(10.98)	16(19.51)	12(14.63)	29(35.37)	30(36.59)	20(24.39)	37(45.12)	82
Pieridae	**12**	**8**	**11**	**19**	**15**	**14**	**10**	**12**	**25**	**26**	**21**	**27**	
Dismorphiinae	2(9.52)	1(4.76)	0	4(19.05)	2(9.529	2(9.52)	2(9.52)	1(4.76)	4(19.05)	7(33.33)	4(19.05)	10(47.62)	21
Coliadinae	14(40)	13(37.14)	17(48.57)	17(48.57)	16(45.71)	13(37.14)	12(34.29)	14(40)	21(60)	22(62.86)	20(57.14)	24(68.57)	35
Pierinae	7(11.29)	1(1.61)	4(6.45)	10(16.13)	6(9.68)	5(8.06)	5(8.06)	4(6.45)	16(25.81)	16(25.81)	11(17.74)	19(30.65)	62
Nynphalidae	**69**	**59**	**51**	**94**	**70**	**62**	**64**	**68**	**94**	**98**	**78**	**115**	
Heliconinae	19(46.34)	17(41.46)	13(31.71)	19(46.34)	12(29.27)	13(31.71)	14(34.15)	16(39.02)	23(56.10)	19(46.34)	13(31.71)	28(68.29)	41
Nymphalinae	16(10.88)	14(9.52)	14(9.52)	21(14.29)	17(11.56)	18(12.24)	11(7.48)	15(10.20)	27(18.37)	27(18.37)	38(25.85)	51(34.69)	147
Limenitidinae	37(25.87)	28(19.58)	30(20.98)	56(39.16)	37(25.87)	33(23.08)	31(21.68)	32(22.38)	56(39.16)	59(41.26)	40(27.97)	90(62.94)	143
Charaxinae	14(21.88)	4(6.25)	3(4.69)	22(34.38)	11(17.19)	7(10.94)	17(26.56)	10(15.63)	26(40.63)	23(35.94)	14(21.88)	38(59.38)	64
Apaturinae	3(27.27)	1(9.09)	1(9.09)	4(36.36)	2(18.18)	3(27.27)	1(9.09)	0	5(45.45)	4(36.36)	4(36.36)	5(45.45)	11
Morphinae	1(10)	1(10)	1(10)	3(30)	1(10)	1(10)	1(10)	3(30)	3(30)	3(30)	1(10)	6(60)	10
Brassolinae	4(22.22)	3(16.67)	6(33.33)	11(61.11)	6(33.33)	5(27.78)	7(38.89)	6(33.33)	9(50)	11(61.11)	7(38.89)	12(66.67)	18
Satyrinae	8(7.41)	6(5.56)	5(4.63)	20(18.52)	15(13.89)	9(8.33)	11(10.19)	8(7.41)	21(19.44)	25(23.15)	16(14.81)	41(37.96)	108
Danainae	4(52.14)	4(57.14)	2(28.57)	4(57.14)	3(42.86)	2(28.57)	4(57.14)	4(57.14)	4(57.14)	6(85.71)	4(57.14)	6(85.71)	7
Ithomiinae	11(23.40)	12(25.53)	6(12.77)	20(42.55)	11(23.40)	12(25.53)	15(31.91)	17(36.17)	21(44.68)	20(42.55)	8(17.02)	30(63.83)	47
Libytheinae	1(50)	1(50)	1(50)	1(50)	1(50)	0	1(50)	1(50)	1(50)	1(50)	1(50)	1(50)	2
Lycaenidae	**36**	**9**	**12**	**71**	**43**	**13**	**11**	**23**	**55**	**97**	**58**	**116**	
Riodininae	18(7.96)	6(2.65)	8(3.54)	64(28.32)	21(9.29)	8(3.54)	0	1(0.44)	54(23.89)	76(33.63)	42(18.58)	125(55.31	226
Theclinae	29(12.61)	6(2.61)	5(2.17)	49(21.30)	33(14.35)	5(2.17)	8(3.48)	28(12.17)	30(13.04)	126(54.78	50(21.74)	150(65.22	230
Polyommatinae	4(9.76)	0	0	3(7.32)	4(9.76)	0	4(9.76)	1(2.44)	5(12.20)	7(17.07)	7(17.07)	10(24.39)	41
TOTAL	207	129	130	352	213	145	160	173	355	482	300	683	1295

NOTE: The numbers in family rows correspond to the total genera in each geographical unit and, in parentheses, the percentage of species per subfamily in relation to the total in México. ETF: represents the total for México ETF

MEX: represents the total for all of México

Table 1 also details the total number of species in the ETF of México for Papilionidae (37), Pieridae (53), Nymphalidae (308), and Lycaenidae (285), and the total number of genera per family for each geographical unit.

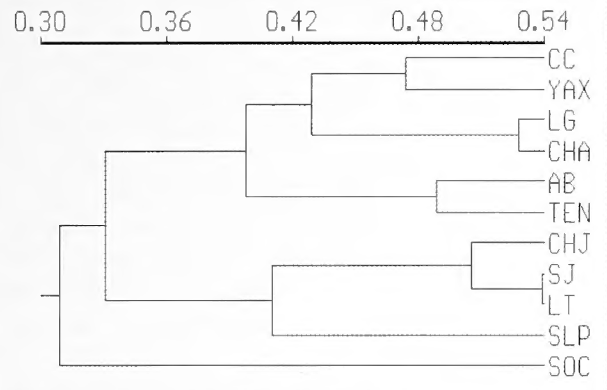

FIG. 2. UPGMA DENDROGRAM OF THE GEOGRAPHICAL UNITS BASED ON THE JACCARD SIMILARITY COEFFICIENT.

The geographical units having the highest number of exclusive species are LT (84), CHJ (40), and SJ (23). When the geographical units were gruped by state, the three in Tabasco (CC-AB-TEN) shared 78 species; in Oaxaca (LG-CHA-SJ), 105; and in Chiapas (CHJ-YAX-SOC) 84. In Chiapas, the units CHJ-SOC share 114 species, while CHJ-YAX share 170; this makes sense since the latter two geographical units belong to the same biogeographical "island" of ETF, while SOC, on the Pacific slope, belongs to a different biogeographical area.

The geographical units SLP and LT, the northernmost localities of ETF, share 243 species, this large figure suggests that both belong to the same biogeographical "island." If the four geographical units having that largest number of species are grouped (LT-SJ-CHJ-SLP), these share only 138 species, again emphasizing the importance of the geographical history of such units, with mixture of species in the northern units having influence over the total number of species.

The UPGMA (unweighted pair-group method using arithmetic averages) dendrogram of all geographical units (Fig. 2) was prepared, based on the Jaccard coefficient to assess the degree of similarity. This similarity between the geographical units was based in part on the synthetic data matrix (Table 2) that groups the species shared by each unit.

As mentioned above, SOC belongs to a distinct geographical "island" of ETF, a fact seen in the dendrogram where it appears as the most dissimilar from all other geographical units. An important group is that whose geographical units have the largest collection effort (SJ-LT-CHJ) and number of species. The remaining group whose geographical units have the lowest number of species, may need more collecting effort. The similarities between LG and CHA, and that between AB and TEN are probably due to their geographical proximity (Fig. 1).

Table 3 compares the numbers of species in various areas of ETF in the Neotropical region, such as Tikal, Guatemala (Austin et al. 1996); Jaru, Manaus, Campinas and Rondonia in Brazil (Brown 1984, Emmel & Austin 1990); Pakitza, Tambopata and Río Napo in Peru

TABLE 2. Synthetic matrix of species shared by the geographical units.

	CC	AB	TEN	CHJ	YAX	SOC	LG	CHA	SJ	LT	SLP
CC	0										
AB	105	0									
TEN	105	85	0								
CHJ	164	110	114	0							
YAX	135	89	98	170	0						
SOC	91	66	70	114	90	0					
LG	118	83	82	139	110	75	0				
CHA	118	84	77	137	105	75	115	0			
SJ	172	116	119	243	160	121	139	142	0		
LT	185	114	122	273	185	119	143	157	293	0	
SLP	130	81	91	168	132	93	102	99	198	243	0

TABLE 3. Butterfly species richness in some localities in the Neotropical region.

FAMILIES	LOCALITIES										
	GUATEMALA	BRASIL				PERU			COSTA RICA		ECUADOR
	Tikal	Jaru	Manaus	Campinas	Rondonia	Pakitza	Tambopata	Río Napo	AL	PE	Misahuallí
Papilionidae	18	23	7	17	18	25	26	26	16	17	36
Pieridae	23	26	7	29	29	31	27	23	26	26	34
Nymphalidae	141	343	137	208	275	371	341	238	219	174	317
Lycaenidae	98	89	50	54	87	181	172	68	*	*	*
Riodinidae	48	196	111	60	203	251	242	153	97	79	*
TOTAL	328	677	312	368	612	859	808	508	358	296	387

NOTE: Asterisks indicate missing data.

ABBREVIATIONS: AL = Atlantic lowland; PE = Pacific evergreen (DeVries 1997).

(Lamas et al. 1991, 1996); several localities in Costa Rica (DeVries 1997); and Misahuallí in Ecuador (Racheli & Racheli 1998). When these data are compared with those from México (Table 1), the species richness of geographical units such as LT or SJ becomes obvious, comparable with that of areas such as Tikal (328 species) or Campinas (368). LT and SJ have the largest know numbers of Pieridae (45 and 41, respectively), for México (and also the Neotropical region).

Conclusions

The ETF of México show a total of 683 species of Papilionoidea (excluding Hesperiidae). Robbins & Opler (1997) state that the higher diversity of butterflies follows the amount of rainfall. The data in this paper include collections made in sites having 1,500 mm minimum average annual rainfall, supporting the empirical observation that wet sites have a large species diversity. However, other parameters must be considered to explain and compare the diversity and richness of species, such as area and topographical or ecological heterogeneity.

Emmel & Austin (1990) discussed the role played by the great "microheterogeneity" present in the locality of Jarú. Environmental heterogeneity is also relevant in our observations; for example SLP and LT are more heterogeneous, giving mixture of species from montane and lowland areas, due to altitude (montane effect) in LT and latitude in SLP.

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Appendix 1: Preliminary list of species. Data for each species are represented in the following format first column is the species name and subsequent columns mention the sites where the butterflies were collected.Asterisks (°)indicate doubtful data.

Taxon	CC	AB	TEN	CHJ	YAX	SOC	LG	CHA	SJ	LT	SLP
Papilionidae											
Battus philenor philenor		X							X	X	X
B. polydamas polydamas	X	X	X	X	X	X	X	X	X	X	X
B. laodamas copanae	X	X	X	X			X	X	X	X	
B. ingenuus				X					X	X	
B. lycidas				X		X			X	X	
Parides photinus	X			X		X			X	X	X
P. montezuma						X				X	X
P. eurimedes mylotes	X	X	X	X	X	X	X	X	X	X	
P. sesostris zestos	X	X	X	X	X		X	X	X	X	
P. panares panares							X	X		X	
P. panares lycimenes	X	X		X					X		
P. erithalion polyzelus	X	X	X	X	X	X	X	X	X	X	
P. iphidamas iphidamas	X		X	X	X	X		X	X	X	
Protographium epidaus epidaus	X	X	X	X					X	X	X
P. philolaus philolaus		X	X	X	X				X	X	X

APPENDIX 1. Continued

Taxon	CC	AB	TEN	CHJ	YAX	SOC	LG	CHA	SJ	LT	SLP
P. agesilaus neosilaus	X		X	X	X				X	X	
P. dioxippus lacandones				X			X				
P. calliste calliste									X	X	X
P. thyastes marchandi				X			X		X	X	
Eurytides salvini				X	X		X				
Protesilaus macrosilaus penthesilaus			X	X				X	X		
Mimoides thymbraeus thymbraeus									X	X	X
M. ilus branchus	X	X	X	X			X	X	X	X	
M. phaon phaon	X		X	X			X	X	X	X	X
Priamides pharnaces					X				X	X	X
P. anchisiades idaeus	X		X	X	X		X	X	X	X	X
P. erostratus erostratinus											X
P. erostratus erostratus					X						
Troilides torquatus tolus									X		
Calaides ornythion ornythion										X	X
C. astyalus pallas				X	X		X		X	X	X
C. androgeus epidaurus			X	X	X	X	X		X	X	X
Heraclides thoas autocles	X	X	X	X	X		X	X	X	X	X
H. cresphontes	X			X		X	X	X	X	X	X
Papilio polyxenes asterius									X	X	X
Pyrrhosticta victorinus victorinus									X	X	X
P. abderus abderus											X
Pieridae											
Enantia lina marion				X	X	X			X		
E. albania albania				X						X	X
E. jethys										X	X
E. mazai mazai									X		
Lieinix nemesis atthis										X	X
Dismorphia amphiona praxinoe	X	X		X	X	X	X			X	X
Dismorphia crisia virgo										X	
D. eunoe eunoe									X		
D. eunoe popoluca										X	
D. theucharila fortunata	X			X			X	X	X	X	
Zerene cesonia cesonia		X	X					X	X	X	X
Anteos clorinde nivifera		X	X	X	X			X	X	X	X
A. maerula lacordairei	X	X	X	X	X			X	X	X	X
Phoebis agarithe agarithe	X	X	X	X	X			X	X	X	X
P. argante argante	X		X	X	X	X	X	X	X	X	X
P. neocypris virgo							X	X	X	X	X
P. philea philea	X	X	X	X	X	X	X	X	X	X	X
P. sennae marcellina	X	X	X	X	X	X	X	X	X	X	X
Rhabdodryas trite ssp.			X	X	X	X		X	X	X	
Aphrissa statira jada	X	X	X	X	X	X	X	X	X	X	X
Abaeis nicippe						X			X	X	X
Pyrisitia dina westwoodi	X	X	X	X	X	X	X		X	X	X
P. lisa centralis	X		X		X	X				X	X
P. nise nelphe	X	X	X	X	X	X	X	X	X	X	X
P. proterpia proterpia	X	X	X	X	X	X	X	X	X	X	X
Eurema agave millerorum	X										
E. albula celata	X	X	X	X	X	X	X	X	X	X	X
E. boisduvaliana	X		X	X	X				X	X	X
E. daira	X	X	X	X	X		X	X	X	X	X
E. mexicana mexicana		X	X	X		X			X	X	X
E. salome jamapa							X		X		X
E. xantochlora xantochlora							X		X	X	

APPENDIX 1. Continued

Taxon	CC	AB	TEN	CHJ	YAX	SOC	LG	CHA	SJ	LT	SLP
Nathalis iole				X	X	X			X	X	X
Kricogonia lyside				X						X	
Hesperocharis costaricensis pasion						X			X	X	
Archonias brassolis aproximata				X			X		X	X	
Charonias theano nigrescens				X	X				X	X	
Catasticta flisa flisa									X	X	X
Catasticta nimbice nimbice										X	X
C. ochracea ochracea										X	
Pereute charops charops									X	X	X
Melete lycimnia isandra	X		X	X		X			X	X	X
M. polyhymnia florinda				X					X		
Glutophrissa drusilla tenuis	X	X	X	X	X		X	X	X	X	X
Pontia protodice									X	X	X
Leptophobia aripa elodia				X		X			X	X	X
Itaballia demophile centralis	X					X			X	X	X
I. pandosia kicaha				X			X	X	X	X	
Pieriballia viardi viardi	X			X	X		X	X	X	X	X
Perrhybris pamela chajulensis				X	X				X		
Ascia monuste monuste	X		X	X	X	X	X	X	X	X	X
Ganyra josephina josepha	X		X		X				X	X	X
G. phaloe tiburtia	X										
Nymphalidae											
Altinote ozomene nox	X					X		X	X	X	
Actinote guatemalena veraecrusis	X	X					X		X	X	
A. guatemalena guatemalena		X	X	X	X						
A. thalia anteas						X					
Philaethria diatonica	X			X					X	X	
Dione juno huascuma	X	X	X	X	X	X	X	X	X	X	X
D. moneta poeyii							X	X	X	X	X
Agraulis vanillae incarnata	X	X	X	X	X	X	X	X	X	X	X
Dryadula phaetusa	X	X	X	X			X	X	X	X	X
Dryas iulia moderata	X	X	X	X	X	X	X	X	X	X	X
Eueides aliphera gracilis	X	X		X	X	X	X	X	X	X	
E. isabella eva	X		X	X			X		X	X	X
E. lineata	X	X		X	X				X	X	X
E. procula asidia	X								X		
E. vibilia vialis	X			X				X		X	
Laparus doris viridis	X	X		X				X	X	X	
Heliconius charitonia vazquezae	X	X	X	X	X	X	X	X	X	X	X
Heliconius cydno galanthus		X		X	X		X	X			
H. erato petiveranus	X	X	X	X	X	X	X	X	X	X	X
H. hecale zuleika	X	X	X						X		
H. hecale fornarina						X					
H. hecalesia octavia				X		X		X	X		
H. hortense			X			X			X	X	X
H. ismenius telchinia	X	X	X	X	X	X	X	X	X	X	X
H. sapho leuce	X	X	X	X	X		X	X	X	X	
H. sara veraepacis		X		X					X		
Euptoieta claudia daunius									X		X
E. hegesia hoffmanni	X	X	X	X	X	X	X	X	X	X	X
Vanessa atalanta rubria										X	X
Cynthia cardui										X	X
C. virginiensis				X						X	X
C. anabella											X
Nymphalis antiopa antiopa											X

APPENDIX 1. Continued

Taxon	CC	AB	TEN	CHJ	YAX	SOC	LG	CHA	SJ	LT	SLP
Polygonia interrogationis										X	
Hypanartia dione						X			X		
H. godmanii				X		X			X	X	X
H. lethe				X		X		X	X	X	X
H. kefersteini											X
Anartia amathea venusta	X	X	X	X	X	X	X	X	X	X	X
A. jatrophae luteipicta	X	X	X	X	X	X	X	X	X	X	X
Siproeta epaphus epaphus	X	X	X	X	X	X	X		X	X	X
S. stelenes biplagiata	X		X	X	X	X	X	X	X	X	X
S. superba superba	X	X	X	X		X			X	X	
Junonia coenia		X							X	X	X
J. evarete	X			X	X	X		X	X	X	X
Chlosyne erodyle erodyle	X	X	X		X	X		X	X	X	
C. gaudialis gaudialis	X	X	X	X	X	X		X	X	X	
C. hippodrome hippodrome			X		X				X	X	X
C. janais	X	X	X	X	X	X	X	X	X	X	X
C. lacinia lacinia	X		X	X	X		X	X	X	X	X
C. marina marina		X									
C. rosita browni											X
Thessalia theona theona	X	X	X	X					X		X
T. theona thekla					X						
Texola elada elada		X									
T. elada ulrica											X
Microtia elva horni								X			X
Phyciodes mylitta mexicana	X		X								
P. vesta graphica					X				X	X	X
P. phaon											X
Phyciodes tharos tharos					X						X
Anthanassa ardys ardys			X							X	X
A. argentea				X			X				X
A. atronia sydra									X		X
A. atronia atronia						X					
A. drusilla lelex	X	X					X	X	X	X	X
A. frisia tulcis					X	X			X	X	X
A. ptolyca ptolyca				X		X					X
A. texana texana											X
A. annulata											X
Tegosa anieta cluvia					X						
T. anieta luka									X		X
T. guatemalena	X			X				X	X	X	
T. similis				X							X
Eresia clara clara			X	X	X		X		X	X	X
E. phillyra phillyra	X	X		X		X	X	X	X	X	X
Castilia eranites mejicana				X				X	X	X	X
C. myia myia	X	X		X	X	X	X	X	X	X	X
C. ofella ofella						X			X		
Historis odius dious	X	X	X		X	X	X		X	X	X
Coea acheronta acheronta	X	X	X	X	X	X	X	X	X	X	X
Baeotus beotus beotus				X							
Smyrna blomfildia datis	X		X	X	X	X	X	X	X	X	X
S. karwinskii				X		X	X		X		X
Colobura dirce dirce	X	X	X	X	X	X	X	X	X	X	X
Tigridia acesta ssp.				X	X						
Biblis hyperia aganisa	X	X	X	X	X	X	X	X	X	X	X
Mestra dorcas amymone	X	X	X	X	X	X			X	X	X
Myscelia cyananthe cyananthe							X				

APPENDIX 1. Continued

Taxon	CC	AB	TEN	CHJ	YAX	SOC	LG	CHA	SJ	LT	SLP
Myscelia cyaniris cyaniris	X	X	X	X	X			X	X	X	X
M. ethusa ethusa		X							X	X	X
Catonephele mexicana	X			X	X	X	X	X	X	X	X
C. numilia esite	X	X	X	X	X	X	X	X	X	X	X
Catonephele cortesi					X						
Nessaea aglaura aglaura	X			X	X			X	X	X	
Eunica alcmena			X	X	X		X		X	X	
E. alpais excelsa				X							
Eunica sydonia caresa				X	X	X					
E. malvina albida	X			X		X					
E. monima	X	X		X	X	X	X	X	X	X	X
E. mygdonia omoa			X	X	X						
E. olympias augusta	X		X	X		X	X		X	X	
E. venusia				X							
E. tatila tatila					X						X
Hamadryas amphinome mexicana	X	X	X	X	X		X	X	X	X	X
H. februa ferentina	X	X	X	X	X	X	X	X	X	X	X
H. feronia farinulenta	X	X	X	X	X	X	X	X	X	X	X
H. fornax fornacalia					X				X		X
H. glauconome glauconome				X				X	X	X	X
H. guatemalena marmarice	X	X			X		X	X	X	X	X
H. guatemalena guatemalena				X					X		
H. iphthime joannae	X		X	X	X	X	X	X	X	X	
H. laodamia saurites	X	X	X	X	X	X	X	X	X	X	
Ectima erycinoides ssp.				X							
Pyrrhogyra edocla edocla				X					X	X	
P. neaerea hypsenor	X	X	X	X	X	X			X	X	
P. otolais otolais	X	X	X	X	X	X			X	X	X
Temenis laothoe hondurensis	X	X	X	X	X		X	X	X	X	X
Epiphile adrasta adrasta									X	X	X
E. hermosa									X		
E. orea plutonia									X	X	
Bolboneura sylphis veracruzana											X
B. sylphis lacandona				X							
Nica flavilla bachiana	X	X	X	X	X	X	X	X		X	X
Dynamine artemisia glauce		X		X					X	X	
D. ate				X							
D. dyonis										X	X
D. postverta mexicana	X	X	X		X		X	X		X	
D. theseus		X									
Diaethria anna	X		X	X		X	X	X	X	X	X
D. astala astala				X		X	X	X	X	X	X
Cyclogramma bacchis										X	
Cyclogramma pandama									X	X	X
Callicore astarte casta								X	X	X	
Callicore astarte patelina				X	X						
C. lyca lyca		X		X			X	X	X	X	
C. texa grijalva	X	X	X				X	X	X	X	
C. texa titania				X	X	X					
C. tolima tehuana									X		
C. tolima pacifica						X					
C. pitheas						X					
Adelpha basiloides basiloides	X	X	X	X	X			X	X	X	X
A. baeotia milleri										X	
A. baeotia oberthurii				X							
A. celerio diademata	X	X	X	X		X			X	X	X

APPENDIX 1. Continued

Taxon	CC	AB	TEN	CHJ	YAX	SOC	LG	CHA	SJ	LT	SLP
Adelpha bredowii eulalia											X
A. cytherea marcia				X			X	X	X		
A. escalantei									X		
A. felderi jarias				X				X	X	X	
A. iphiclus iphicleola	X			X	X		X		X	X	
A. diazi	X							X		X	
A. ixia leucas	X			X					X	X	
A. leuceria leuceria				X		X			X	X	X
A. leucerioides leucerioides										X	
A. lycorias melanthe	X								X	X	X
A. naxia epiphicla				X	X	X			X	X	
A. paroeca emathia										X	
A. phylaca phylaca	X		X	X			X		X	X	X
Adelpha pithys										X	
A. salmoneus salmonides										X	
A. serpa massilia	X		X	X					X	X	X
A. zalmona sophax				X							
A. fessonia fessonia											X
Basilarchia archippus hoffmanni									X	X	X
Marpesia chiron marius	X	X	X	X	X	X	X	X	X	X	X
M. corita corita				X		X		X	X	X	
M. harmonia	X	X	X	X	X	X	X	X	X	X	
M. petreus tethys	X	X	X	X	X	X	X		X	X	X
M. zerynthia dentigera						X		X	X		X
Archaeoprepona amphimachus amphiktion	X		X	X	X	X	X				
A. demophon centralis	X			X	X	X	X	X	X	X	X
A. demophoon gulina	X	X		X	X	X	X		X	X	X
A. meander phoebus				X	X						
A. phaedra aelia									X		
Prepona deiphile brooksiana									X		
P. deiphile escalantiana										X	X
P. dexamenes medinai				X							
P. laertes octavia	X			X	X		X		X	X	
P. pylene philetas				X					X		
Agrias aedon rodriguezi				X							
A. amydon oaxacata				X			X				
Zaretis callidryas	X								X	X	
Z. itus ellops	X	X		X			X	X	X	X	
Siderone galanthis ssp.				X						X	
S. syntiche syntiche	X				X	X	X	X	X		
Anaea troglodyta aidea	X					X		X	X	X	X
Consul electra electra	X	X	X	X	X		X		X	X	X
C. fabius cecrops	X	X	X	X	X	X	X		X	X	X
Fountainea eurypyle confusa	X		X	X	X		X	X	X	X	X
F. glycerium glycerium									X	X	X
F. halice martinezi									X		
F. ryphea ryphea									X	X	
Memphis artacaena	X			X	X		X			X	
M. aureola									X		
M. dia ssp.									X		
M. forreri									X	X	X
M. hedemanni				X						X	
M. herbacea				X							
M. mora orthesia	X			X			X				X
M. phila boisduvali	X			X					X	X	X
M. neidhoeferi				X					X	X	

APPENDIX 1. Continued

Taxon	CC	AB	TEN	CHJ	YAX	SOC	LG	CHA	SJ	LT	SLP
Memphis oenomais				X			X	X	X	X	X
M. philumena xenica							X	X	X	X	
M. pithyusa	X			X	X	X	X	X	X	X	X
M. proserpina				X			X	X	X	X	
M. xenocles carolina							X				
M. perenna perenna						X					
Asterocampa idyja argus				X					X	X	X
Doxocopa cyane mexicana									X		
D. laure laure	X	X	X	X	X	X			X	X	X
D. laurentia cherubina	X			X		X			X	X	X
D. pavon theodora	X			X	X	X	X		X	X	X
Morpho achilles montezuma	X	X	X	X			X	X	X	X	X
M. achilles octavia					X	X					
Pessonia luna luna				X				X	X	X	
Iphimedeia telemachus justitiae				X							
I. telemachus ssp.										X	
I. telemachus oaxacensis								X	X		
Dynastor darius stygianus				X							
D. macrosiris strix				X						X	X
Opsiphanes boisduvalii	X		X	X					X	X	X
O. cassiae			X				X		X	X	X
O. tamarindi	X	X		X	X	X	X	X	X	X	X
O. invirae fabricii	X	X	X	X	X	X	X	X	X	X	X
O. quiteria quirinus				X			X	X	X	X	
Caligo atreus uranus				X	X	X	X	X	X	X	X
C. oileus scamander			X	X	X		X	X		X	
C. prometheus memnon	X	X	X	X	X	X	X	X	X	X	
Eryphanis aesacus aesacus			X	X	X	X			X	X	X
Narope cyllastros testacea				X					X	X	
Pierella luna rubecula	X	X	X	X	X		X	X	X	X	
Manataria maculata				X		X			X	X	X
Cepheuptychia glaucina				X	X				X	X	X
Chloreuptychia sericeella				X				X	X	X	
Cissia confusa					X					X	X
C. labe				X			X		X	X	
C. terrestris			X						X		
Cyllopsis hedemanni hedemanni									X		
C. hedemanni tamaulipensis											X
C. hilaria				X							
C. suivalens escalantei									X		
C. pyracmon						X					
C. gemma freemani											X
C. dospassosi											X
Euptychia mollina				X					X	X	X
Hermeuptychia hermes	X			X	X	X	X	X	X	X	X
H. alcinoe										X	
Oxeoschistus hilara hilara						X					
Magneuptychia libye	X	X	X	X	X	X	X		X	X	
Megeuptychia antonoe				X	X				X	X	
Pareuptychia binocula metaleuca	X			X	X		X	X	X	X	X
P. interjecta		X									
P. ocirrhoe	X		X	X	X	X	X	X	X	X	X
Pseudodebis zimri				X	X					X	
Satyrotaygetis satyrina										X	
Splendeuptychia kendalli					X						X
Paramacera xicaque xicaque											X

APPENDIX 1. Continued

Taxon	CC	AB	TEN	CHJ	YAX	SOC	LG	CHA	SJ	LT	SLP
Taygetis kerea kerea							X				
T. leuctra				X							
T. mermeria excavata			X	X	X				X	X	
T. uncinata									X	X	
T. virgilia		X		X	X	X	X		X	X	X
T. weymeri				X							
T. thamyra				X	X		X	X		X	X
Vareuptychia usitata pieria	X	X		X	X		X	X	X	X	X
V. themis										X	
V. similis		X				X				X	
V. undina	X									X	
Yphthimoides renata disaffecta	X			X	X		X	X	X	X	
Dioriste tauropolis tauropolis						X			X	X	X
Pedaliodes dejecta circumducta									X		
Danaus eresimus montezuma	X	X		X	X		X	X	X	X	X
D. gilippus thersippus	X	X	X	X	X		X	X	X	X	X
D. plexippus plexippus	X	X	X	X		X	X	X	X	X	X
Lycorea halia atergatis	X	X		X	X	X	X	X	X	X	X
L. ilione albescens										X	
Anetia thirza thirza										X	
Tithorea harmonia hippothous	X			X	X		X		X	X	
T. tarricina duenna									X		X
Aeria eurimedea pacifica		X	X	X	X	X	X		X	X	
Olyras crathis theon									X	X	
Melinaea lilis flavicans	X	X		X				X	X	X	
M. lilis imitata						X					
Mechanitis lysimnia utemaia	X		X	X	X		X	X	X	X	
M. menapis doryssus	X	X		X	X	X	X	X	X	X	
M. polymnia lycidice	X	X	X	X	X	X	X	X	X	X	
Hyposcada virginiana virginiana		X		X		X		X	X		
Oleria paula	X			X	X	X	X	X	X	X	X
Napeogenes tolosa tolosa		X		X	X		X	X	X	X	
Hypothyris euclea valora										X	
H. lycaste dionaea				X	X	X		X	X	X	
Ithomia leila				X			X	X	X	X	
I. patilla patilla	X	X		X	X	X	X	X	X	X	
Callithomia hezia hedila							X	X	X		
C. hezia wellingi				X							
Dircenna dero ssp.	X	X		X			X	X			
D. jemina ssp.									X		
D. klugii klugii	X	X		X		X		X	X	X	X
Episcada salvinia salvinia						X			X		
Pteronymia artena artena										X	
P. cotytto	X	X		X			X	X	X	X	X
P. simplex fenochioi											X
Godyris zavaleta sosunga		X	X	X							
Hypomenitis annette annette										X	X
Greta morgane oto	X	X	X	X	X	X	X	X	X	X	X
G. nero nero			X	X	X	X	X	X	X	X	X
Hypoleria lavinia cassotis				X			X	X		X	
Libytheana carinenta mexicana	X	X	X	X	X		X	X	X	X	X
Lycaenidae											
Euselasia cataleuca				X					X	X	
E. chrysippe				X							
E. regipennis regipennis				X							
E. sergia sergia				X					X	X	

APPENDIX 1. Continued

Taxon	CC	AB	TEN	CHJ	YAX	SOC	LG	CHA	SJ	LT	SLP
Euselasia procula				X							
E. hieronymi hieronymi									X	X	X
E. inconspicua									X		
E. pusilla									X	X	
E. eubule eubule									X	X	X
E. aurantiaca aurantiaca				X		X			X	X	
Hades noctula				X					X	X	
Perophthalma tullius lasus				X						X	
Leucochimona vestalis vestalis				X					X	X	
L. lepida nivalis	X			X	X				X	X	X
Mesosemia telegone telegone	X	X		X	X				X	X	X
M. gaudiolum				X						X	
M. gemina								X	X	X	
Eurybia patrona persona				X							
E. lycisca			X	X					X	X	
E. halimede elvina	X	X		X	X				X	X	
Hermathena oweni										X	
Diophtalma lagora iphias						X					
Napaea eucharila picina				X							
N. theages theages				X							
N. umbra umbra					X				X	X	X
Cremna actoris				X							
C. thasus subrutila				X						X	
Lyropteryx lyra cleadas				X					X		
Ancyluris jurgensenii montezuma				X					X	X	
A. inca mora				X					X	X	
Rhetus arcius thia	X		X	X	X	X			X	X	X
R. periander naevianus				X					X		
Isapis agyrtus hera				X					X		
Brachyglenis dodone				X							
Notheme erota diadema				X	X					X	
Lepricornis melanchroia				X					X	X	
Calephelis nemesis nemesis										X	
C. mexicana				X							
C. fulmen									X	X	X
C. stallingsi										X	X
C. huasteca									X		X
C. acapulcoensis									X		
C. yucatana									X		
C. perditalis perditalis											X
C. montezuma											X
C. laverna laverna						X					
Charis gynaea zama				X	X					X	
C. velutina					X				X	X	
Chalodeta chaonitis				X							
Caria ino melicerta									X	X	X
C. domitianus vejento				X							
C. rhacotis rhacotis					X					X	
C. lampeto				X					X		
Baeotis zonata simbla					X				X	X	X
B. sulphurea macularia					X						
B. sulphurea sulphurea											X
Lasaia meris				X							
L. agesilas callaina	X			X					X	X	X
L. sessilis	X										
L. maria anna				X	X					X	X

APPENDIX 1. Continued

Taxon	CC	AB	TEN	CHJ	YAX	SOC	LG	CHA	SJ	LT	SLP
*L. narses**						X					
L. sula peninsularis											X
Melanis pixe pixe	X	X	X	X	X	X			X	X	X
M. cephise cephise										X	
M. cephise huasteca											X
Mesene croceella				X					X	X	X
M. margaretta margaretta				X		X				X	X
Xenandra caeruleata				X						X	
Chimastrum argenteum argenteum				X							
Symmachia rubina rubina				X						X	
S. accusatrix									X	X	X
Symmachia probetor championi									X	X	X
S. tricolor hedemanni				X					X	X	
Pterographium sagaris tyriotes										X	
Sarota gamelia										X	
S. acanthoides myrtea										X	X
S. chrysus dematria				X					X	X	X
Anteros formosus micon				X							
A. carausius carausius	X				X				X	X	X
Calydna lusca venusta										X	
C. sturnula hegias										X	X
C. sinuata										X	
Emesis aurimna				X						X	
E. saturata			X						X		X
E. liodes										X	
E. mandana furor				X					X	X	X
E. vulpina	X				X				X		
E. fatimella nobilata				X							X
E. tenedia tenedia	X			X	X				X	X	X
E. lupina				X						X	
E. ocypore aethalia				X							
E. zela zela									X		
E. emesia emesia				X						X	X
E. cypria paphia									X		
E. tegula										X	
E. zela cleis											X
Argyrogrammana holosticta	X			X						X	X
Pseudonymphidia clearista									X		X
Pachythone gigas				X							
Apodemia multiplaga										X	
A. hypoglauca hypoglauca										X	X
A. walkeri				X							
Thisbe irenea belides	X	X							X	X	
T. lycorias lycorias	X	X	X	X					X	X	X
Lemonias caliginea			X							X	
L. agave									X	X	X
Juditha molpe	X	X	X	X	X				X	X	
Synargis calyce mycone	X			X	X	X			X	X	
S. ethelinda nymphidioides										X	
S. nycteus										X	
Menander menander purpurata	X		X	X	X				X	X	
Pandemos godmanii									X		X
Calospila pelarge				X						X	
C. sudias	X			X	X				X	X	
Theope pedias isia				X							
T. virgilius virgilius				X					X		X

APPENDIX 1. Continued

Taxon	CC	AB	TEN	CHJ	YAX	SOC	LG	CHA	SJ	LT	SLP
Theope eupolis										X	
T. cratylus										X	
T. publius	X				X						
T. eleutho										X	X
T. mania										X	
T. diores											X
Calociasma lilina										X	
Nymphidium ascolia ascolides				X							
Brephidium exilis exilis											X
Leptotes marina										X	X
L. cassius striata	X			X	X		X		X	X	X
Zizula cyna cyna	X			X	X		X		X		X
Hemiargus ceraunus	X				X		X	X	X	X	X
H. isola isola									X		
H. huntingtoni hannoides										X	
Everes comyntas	X			X	X		X		X	X	X
E. amyntula amyntula										X	
Celastrina argiolus gozora										X	X
Eumaeus childrenae				X	X				X	X	
E. toxea	X			X	X				X	X	X
Paiwarria antigonus					X						
Theorema eumenia				X					X	X	
"Thecla" (busa group) busa				X					X	X	
Evenus regalis				X	X					X	X
E. coronata				X							
E. batesii										X	
"Thecla" (gibberosa group) barajo				X				X	X	X	
"Thecla" (eunus group) eunus										X	
Allosmaitia strophius										X	X
Pseudolycaena damo	X		X	X	X	X	X		X	X	X
Arcas imperialis		X		X					X		
A. cypria				X	X				X	X	X
Theritas mavors				X		X			X	X	X
"Thecla" (hemon group) augustinula									X		
"Thecla" (hemon group) theocritus				X						X	
"Thecla" (hemon group) hemon				X							
"Thecla" (hemon group) lisus										X	
Atlides gaumeri										X	
A. polybe			X	X						X	X
A. inachus										X	
A. carpasia										X	X
A. halesus											X
*A. caranus**											X
Radissima umbratus										X	
"Thecla" (ligurina group) ligurina				X			X			X	
"Thecla" (ligurina group) lyde										X	
Denivia theocritus											X
Contrafacia ahola										X	
C. imma										X	X
Thereus cithonius										X	
T. oppia	X									X	
T. ortalus										X	
Arawacus togarna	X	X	X	X	X		X	X	X	X	
A. sito	X	X	X	X	X	X		X	X	X	X
A. jada	X										X
Rekoa meton	X			X	X				X	X	X

APPENDIX 1. Continued

Taxon	CC	AB	TEN	CHJ	YAX	SOC	LG	CHA	SJ	LT	SLP
Rekoa palegon	X			X	X			X	X	X	X
R. zebina										X	
R. marius	X									X	
R. stagira										X	
Ocaria petelina										X	
O. thales				X	X						
O. ocrisia										X	X
Magnastigma elsa										X	
Chlorostrymon simaethis				X	X					X	X
C. telea										X	X
Cyanophrys goodsoni										X	X
C. amyntor				X						X	X
C. fusius				X						X	X
C. herodotus					X			X		X	X
C. miserabilis	X									X	X
C. longula										X	
Panthiades bitias	X	X		X	X		X		X	X	X
P. ochus				X				X	X	X	X
P. bathildis	X	X	X	X	X		X	X	X	X	X
P. phaleros				X	X					X	
Oenomaus ortygnus				X	X					X	X
O. atesa				X							
Parrhasius polibetes				X					X	X	X
P. orgia				X					X	X	
P. moctezuma										X	X
Michaelus jebus				X						X	X
M. thordesa				X						X	
M. hecate										X	
M. vibidia										X	
M. zenaida					X						
Ignata gadira									X	X	
I. nr. gadira										X	
I. norax									X	X	
Strymon melinus										X	X
S. albata	X									X	X
S. alea									X		
S. bazochii				X	X					X	X
S. mulucha								X		X	
S. yojoa	X			X	X					X	X
S. cestri					X			X		X	X
S. astiocha										X	
S. istapa					X			X		X	X
S. ziba	X				X					X	
S. nr. megarus #1										X	
S. serapio					X					X	
*S. basalides**											X
Lamprospilus collucia										X	
"Thecla" (aruma group) galliena										X	
Kisutam syllis	X				X			X		X	
K. hesperitis				X	X			X		X	
K. ceromia	X										
K. denarius									X	X	
K. guzanta				X					X	X	
K. sethon											X
"Thecla" (camissa group) vespasianus							X		X		
Electrostrymon mathewi										X	X

APPENDIX 1. Continued

Taxon	CC	AB	TEN	CHJ	YAX	SOC	LG	CHA	SJ	LT	SLP
Electrostrymon sangala					X					X	X
E. canus										X	
Calycopis calus										X	
C. demonassa	X			X						X	X
C. atnius	X							X			
C. clarina	X								X	X	
C. isobeon	X			X		X	X	X		X	X
C. susanna										X	
C. drusilla	X										
C. trebula				X	X			X		X	
Tmolus echion	X			X	X			X		X	X
T. crolinus										X	
T. cydrara				X					X	X	
Crimsinota phobe										X	
"Tmolus" (heraldica group) heraldica	X										
"Thecla" (empusa group) halciones	X							X			
"Thecla" (keila group) keila										X	
Siderus philinna										X	
S. gargophia										X	
S. caninius								X			
S. thoria										X	
Aubergina paetus										X	
"Thecla" (mycon group) mycon	X			X	X		X	X	X	X	X
"Thecla" (tephraeus group) tephraeus			X						X		
"Thecla" (tephraeus group) syedra				X				X			
"Thecla" (tephraeus group) ambrax									X		
Ministrymon clytie										X	X
M. arola					X					X	
M. una									X	X	
M. inoa										X	
M. phrutus										X	X
M. azia					X				X	X	
Janthecla janthodonia										X	
J. janthina	X			X				X	X	X	
Ipidecla schausi										X	
Brangas neora					X					X	X
B. getus										X	
B. coccineifrons				X				X		X	
B. carthaea										X	
"Thecla" (cupentus group) cupentus			X								
Chalybs janias				X		X			X	X	X
C. hassan										X	
"Thecla" (theia group) theia										X	
Hypostrymon critola		X						X			
Iaspis nr castitas	X									X	
I. temesa	X						X	X			
Nesiostrymon calchinia										X	
N. celona										X	
N. dodava										X	
Erora carla								X		X	
E. opisena										X	
E. muridosca										X	
"Thecla" (ares group) semones										X	
Caerofethra carnica								X		X	
Celmia celmus								X		X	X
"Thecla" (color group) conoveria										X	

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HISTOIRE GÉNÉRALE ET ICONOGRAPHIE DES LÉPIDOPTÈRES ET DES CHENILLES DE L'AMÉRIQUE SEPTENTRIONALE BY BOISDUVAL & LE CONTE (1829-[1837]): ORIGINAL DRAWINGS USED FOR THE ENGRAVED PLATES AND THE TRUE IDENTITIES OF FOUR FIGURED TAXA

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ABSTRACT. A set of 149 Lepidoptera drawings is currently deposited in the Thomas Cooper Library, University of South Carolina. Forty of the 55 butterfly drawings include figures that were copied for the engraved plates in *Histoire Générale et Iconographie des Lépidoptères et des Chenilles de l'Amérique Septentrionale* (Boisduval & Le Conte 1829-[1837]). Identifications are provided herein for the 80 butterfly species in these drawings, as well as manuscript notes that likely accompanied 21 other drawings reproduced in *Histoire Générale*. *Pieris cleomes* Boisduval & Le Conte is shown to be synonymous with *Ascia monuste phileta* (Fabricius). The figures identified as *Thecla favonius* (J. E. Smith) represent both *Satyrium favonius* and *Strymon melinus* (Hübner). The figures identified as *Libythea motya* (Hübner) represent *Libytheana motya* and *Libytheana carinenta bachmanii* (Kirtland). Also included are remarks about the identity of *Melitaea ismeria* Boisduval & Le Conte and the validity of the Boisduval type specimens of North American Lepidoptera.

Additional key words: John Abbot, Émile Blanchard, Paul Duménil, Georgia, South Carolina, type locality.

I recently traced the history of a set of 149 Lepidoptera drawings now deposited in the Thomas Cooper Library, University of South Carolina (Calhoun 2003). These were rendered in graphite and watercolor by at least four artists: English naturalist John Abbot (1751-ca.1840), who resided in Virginia and Georgia from 1773 until his death; French zoologist Émile (or Charles Émile) Blanchard (1819-1900); French engraver and publisher Paul C. R. C. Duménil (1779-?); and probably American naturalist John E. Le Conte, Jr. (1784-1860). My analysis of these drawings confirmed the claim of art historian Vivian Rogers-Price (1983) that some were copied for plates in *Histoire Générale et Iconographie des Lépidoptères et des Chenilles de l'Amérique Septentrionale* [General History and Iconography of the Lepidoptera and the Caterpillars of Northern America] by Jean B. A. D. de Boisduval and J. E. Le Conte, Jr., published in 26 livraisons from 1829 to 1837 (usually cited as [1833]). After the publication of *Histoire Générale*, Boisduval retained these drawings for many years and they eventually passed into the hands of lepidopterist Charles M. Oberthür. Oberthür died in 1924 and the drawings have not been examined by another lepidopterist since that time.

These 149 drawings are of great relevance to American lepidopterists. The Thomas Cooper Library has digitized all 149 drawings and made them available for viewing on the Internet (USC 2003). As part of their study, I was afforded the opportunity to offer identifications and other pertinent information. Due to the ephemeral nature of Internet web sites, I have decided to also present this data in print and incorporate many additional details. I also provide information on three sets of surviving manuscript notes by John Abbot that contain entries relevant to published plates in Boisduval & Le Conte (1829-[1837]). Evidence from this research clarifies the origin of specimens figured in Boisduval & Le Conte (1829-[1837]) and resolves the status of *Pieris cleomes* Boisduval & Le Conte, as well as the butterflies figured as *Thecla favonius* (J. E. Smith) and *Libythea motya* (Hübner). Further evidence regarding the identity of *Melitaea ismeria* Boisduval & Le Conte augments Calhoun (2003).

MATERIALS AND METHODS

The butterfly drawings at the University of South Carolina were examined (in person and through digital scans) and compared with the published plates in Boisduval & Le Conte (1829-[1837]). Also consulted were the plates in Smith & Abbot (1797), as well as original drawings and manuscript notes by John Abbot deposited in the Alexander Turnbull Library (Wellington, New Zealand), the Houghton Library (Harvard University), and The Natural History Museum, London. Inscriptions on the drawings were compared with the known handwriting of Abbot, Boisduval, and Le Conte. The National Museum of Natural History (Washington, D. C.) and The Natural History Museum, London, were searched for relevant specimens from Boisduval's collection.

RESULTS

Original butterfly drawings. Fifty-five of the

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TABLE 1. Butterfly species depicted in original drawings at the Thomas Cooper Library, University of South Carolina. B&L = Boisduval & Le Conte (1829-[1837]). Figures: D = dorsal, V = ventral, m = male, f = female, L = larva, P = pupa.

No.	Artist	Species depicted	Figures	B&L plate	Figures copied for B&L	Artist credited on B&L plate	B&L name
1	Abbot	*Papilio cresphontes* Cramer	Df,Vf,L,P	12,13	Df,Vf,L,P	Abbot	*Papilio Thoas*
NOTES: drawing has a penciled reference to B&L Plates 12 and 13.							
2	Abbot	*Eurytides marcellus* (Cramer)	Dm,Vm,L,P	2	Dm,Vm,L,P	Abbot	*Papilio Marcellus*
NOTES: depicts the summer form "lecontei" (Rothschild & Jordan), named in honor of B&L coauthor J. E Le Conte. Includes Abbot's inscription, "Autumnal Ajax."							
3	Abbot	*Eurytides marcellus* (Cramer)	Dm,Df,Vm,L,P	1	Dm,Vm,L,P	Abbot	*Papilio Ajax*
NOTES: depicts the spring form "marcellus" and has a penciled reference to B&L Plate 1. Includes Abbot's inscription, "Spring Ajax." Drawing was figured by Rogers-Price (1983).							
4	Duménil?	*Eurytides celadon* (Lucas)	Df, Vf	3	Df,Vf	Abbot	*Papilio Sinon*
NOTES: the style seems consistent with drawing 37 that Boisduval attributed to Duménil.							
5	Abbot	*Papilio polyxenes* (Fabricius)	Df	—	—	—	—
NOTES: includes Abbot's inscription "Ni Female."							
6	Abbot	*Papilio polyxenes* (Fabricius)	Dm,Vm,L,P	4	Dm,Vm,L,P	Abbot	*Papilio Asterias*
NOTES: includes a penciled reference to B&L Plate 4. Includes Abbot's inscription "Ni Male Troilus."							
7	Abbot	*Ascia monuste* (Linnaeus)	Dm,Df,Vm,L,P	16	Dm,Df,Vf,L,P	Abbot	*Pieris Cleomes*
NOTES: includes a penciled reference to B&L Plate 16, which was copied from this drawing and another from Abbot with a hostplant (see text). Figures in this drawing were probably used for the original description of *P. cleomes*. See Figs 10, 11.							
8	Abbot	*Phoebis sennae* (Linnaeus)	Df,Dm,Vf,L,P	24	Df,Dm,Vf,L,P	Abbot	*Callidryas Eubule*
NOTES: includes a penciled reference to B&L Plate 24 and Abbot's inscription, "Eubule." The ventral female on B&L Plate 24 was misidentified as a male. Scudder (1888-1889, Pl. 76, fig. 2) copied the larva. Holland (1898, Pl. 2, fig. 2) and Klots (1951, Pl. 5, fig. 25) reproduced Scudder's larva.							
9	Abbot	*Zerene cesonia* (Stoll)	Dm,Df,Vf,L,P	22	Dm,Df,Vf,L,P	Abbot	*Colias Coesonia*
NOTES: includes a penciled reference to Plate 22, which was probably copied from this drawing and another from Abbot with duplicate figures and a hostplant. Although the ventral figure is identified on the B&L plate as a male, the corresponding figure in this drawing appears to be a female.							
10	Abbot	a. *Parrhasius m-album* (B&L)	Dm,Df,Vm,L,P	27	Dm,Df,Vm,L,P	Abbot	*Thecla Psyche*
		b. *Strymon melinus* (Hübner)	Dm,Vm,L,P	—	—	—	—
NOTES: the figures of *P. m-album* were probably consulted for the original description of *T. psyche*. Includes a penciled reference to B&L Plate 27 and figure numbers used on the plate. The hostplant "*smilax*" is written below the figures of *S. melinus*. Although Oberthür (1920) believed these figures of *S. melinus* were copied for B&L plate 28 of *T. hyperici*, they are not analogous.							
11	Abbot	a. *Callophrys niphon* (Hübner)	Df,Vf,L,P	33	Df,Vf,L,P	Abbot	*Thecla Niphon*
		b. *Satyrium titus* (Fabricius)	Dm,Df,Vf,L,P	34	Dm,Df,Vf,L,P	Abbot	*Thecla Mopsus*
		c. *Callophrys gryneus* (Hübner)	Dm,Vf,L,P	33	Dm,Vf,L,P	Abbot	*Thecla Smilacis*
NOTES: the figures of *C. gryneus* were probably consulted for the original description of *T. smilacis*. Adult figures of *S. titus* from this drawing and the ventral male of Duménil's drawing 13 were used to illustrate the species on B&L Plate 34. Le Conte wrote "Pine" below *C. niphon*, "Oak, *Eupatorium coelestinum*" below *S. titus*, and "*Smilax*" below *C. gryneus*. These plants were reported as hosts for these butterflies in B&L. Scudder (1888-1889) copied the pupa of *C. niphon* (Pl. 84, fig. 40), the larva and pupa of *S. titus* (Pl. 75, fig. 35; Pl. 84, fig. 37), and the larva and pupa of *C. gryneus* (Pl. 75, fig. 31; Pl. 84, fig. 30). Holland (1898, Pl. 5, figs. 30, 37 & 40) and Klots (1951, Pl. 5, fig. 14) reproduced some of Scudder's figures. See Fig. 4.							
12	Abbot	a. *Satyrium liparops* (Le Conte)	Df,Vf,L,P	31	Df,Vf,L,P	Abbot	*Thecla Liparops*
		b. *Callophrys henrici* (Grote & Robinson)	Dm,Df,Vf,L,P	31	Df,Vf,L,P	Abbot	*Thecla Irus*
NOTES: the figures of *S. liparops* were used for the original description of *Thecla liparops*. Le Conte wrote "Oak, Chestnut" below the figures of *S. liparops* (mentioned by Scudder (1888-1889) and in his notes at Harvard). "*Vaccinium*" is written below the figures of *C. henrici*, which corresponds to the mention of "*vaccinium*" as a hostplant of this species in B&L. *C. henrici* was not described until 1867 and was often confused with *C. irus* in earlier literature. Scudder (1888-1889, Pl. 75, fig. 28) copied the larva of *C. henrici* (as "*Incisalia irus*"). See Figs. 3, 6.							
13	Duménil?	a. *Satyrium titus* (Fabricius)	Dm,Vm	34	Vm	Abbot	*Thecla Mopsus*
		b. *Strymon melinus* (Hübner)	Dm,Vm	—	—	—	—
		c. *Paectes pygmaea* (Hübner)	Dm	—	—	—	—
NOTES: the ventral male of *S. titus* from this drawing and the adults of Abbot's drawing 11 were used to illustrate the species on B&L Plate 34.							

TABLE 1. Continued

No.	Artist	Species depicted	Figures	B&L plate	Figures copied for B&L	Artist credited on B&L plate	B&L name
14	Blanchard	a. *Calycopis cecrops* (Fabricius)	Dm,Df,Vm,Vf	35	Dm,Df,Vm,Vf	Abbot	*Thecla Poeas*
		b. *Hemiargus ceraunus* (Fabricius)	Dm,Df,Vf	35	Dm,Df,Vf	Abbot	*Argus Pseudoptiletes*
NOTES: entire drawing was copied for B&L Plate 35 in the same layout. Figures of *H. ceraunus* accompanied the original description of *A. pseudoptiletes* and are consistent with the Floridian *H. c. antibubastus* (Hübner).							
15	Blanchard	a. *Lycaena hyllus* (Cramer)	Dm,Df,Vm	38	Dm,Df,Vm	Abbot	*Polyommatus Thoe*
		b. *Lycaena epixanthe* (B&L)	Df,Vm	38	Df,Vm	Abbot	*Polyommatus Epixanthe*
NOTES: entire drawing was copied for B&L Plate 38 in the same layout. Figures of *L. epixanthe* accompanied the original description of *P. epixanthe*.							
16	Abbot	a. *Celastrina ladon* (Cramer)	Dm,Df,Vm,L,P	36	Dm,Df,Vm,L,P	Abbot	*Argus Pseudargiolus*
		b. *Cupido comyntas* (Godart)	Dm,Df,Vm,L,P	36	Dm,Df,Vm,L,P	Abbot	*Argus Comyntas*
NOTES: the figures of *C. ladon* were consulted for the original description of *A. pseudargiolus*. Includes Abbot's inscription of "*Argiolus*." Scudder (1888-1889, Pl. 75, figs. 29, 44; Pl. 84, figs. 42, 43) copied all the larvae and pupae that he said were "formerly used in Boisduval and LeConte's iconography." Holland (1898, Pl. 5, figs. 42, 43) and Klots (1951, Pl. 6, fig. 16) reproduced some of Scudder's figures. Rogers-Price (1983) figured the entire drawing.							
17	Blanchard	*Calephelis virginiensis* (Guérin-Méneville)	Dm,Vm	37	Dm,Vm	Abbot	*Nymphidia Pumila*
NOTES: figures accompanied the original description of *N. pumila* and were combined with Abbot's figures of *Feniseca tarquinius* (Fabricius) on B&L Plate 37.							
18	Abbot	*Danaus plexippus* (Linnaeus)	Dm,Vm,L,P	40	Dm,Vm,L,P	Abbot	*Danais Archippus*
NOTES: Rogers-Price (1983) figured the entire drawing.							
19	Abbot	*Danaus gilippus* (Cramer)	Df,Vf,L,P	39	Df,Vf,L,P	Abbot	*Danais Berenice*
NOTES: includes Abbot's inscription of "*Gillippus*."							
20	Blanchard	*Heliconius charithonia* (Linnaeus)	Dm,Vm	41	Dm,Vm	Blanchard	*Heliconia Charitonia*
NOTES: entire drawing was copied for B&L Plate 41 in the same layout. Based in the width of the yellow bands, the figures probably represent the Floridian subspecies *H. c. tuckeri* W. P. Comstock & F. M. Brown.							
21	Abbot	*Agraulis vanillae* (Linnaeus)	Dm,Df,Vf,L,P	42	Df,Vf,L,P	Abbot	*Agraulis Vanillae*
NOTES: drawing has penciled reference to B&L Plate 42, as well as figure legends used on the published plate. It has an attribution to Abbot in Boisduval's hand ("abbot Pinxit.") and includes Abbot's inscription of "*Passiflora*," probably in reference to the name *Papilio passiflorae* of Smith & Abbot (1797). This name was crossed out and Le Conte wrote "*vanillae*" below it. Rogers-Price (1983) figured the entire drawing.							
22	Abbot	*Speyeria idalia* (Drury)	Df,Vf	43	Df,Vf	"Leconte"	*Argynnis Idalia*
NOTES: style is consistent with Abbot, but credited to Le Conte on B&L Plate 43. Abbot is known to have illustrated this species at least one other time; a single male that was "Met with by Mr. Elliot [Stephen Elliott] in his journey to the mountains" (drawing and notes in The Natural History Museum, London). Strangely, the text in B&L did not refer to the occurrence of the species in Virginia or Georgia. References to New York and Jamaica were probably derived from Cramer ([1775]). The paper used for this drawing differs slightly from other Abbot drawings in this set, suggesting that it was original rendered for a different set.							
23	Blanchard	a. *Boloria selene* (Denis & Schiffermüller)	Df,Vf	45	Df,Vf	Blanchard	*Argynnis Myrina*
		b. *Speyeria cybele* (Fabricius)	Df,Vf	45	Df,Vf	Blanchard	*Argynnis Cybele*
		c. *Boloria bellona* (Fabricius)	Df,Vf	45	Df,Vf	Blanchard	*Argynnis Bellona*
NOTES: signed by Blanchard. Entire drawing was copied for Plate 45 in the same layout. The figures represent the eastern North American subspecies *B. s. myrina* (Cramer), *S. c. cybele*, and *B. b. bellona*.							
24	Abbot	a. *Chlosyne gorgone* (Hübner)	Df,Vf,L,P	46	Df,Vf,L,P	Abbot	*Melitaea Ismeria*
		b. *Euptoieta claudia* (Cramer)	Df,Vf,L,P	44	Df,Vf,L,P	Abbot	*Argynnis Columbina*
NOTES: the figures of *C. gorgone* were used for the original description of *M. ismeria* (Calhoun 2003) (see text). The larva in this drawing is not accurately referable to any species, but conceptually resembles that of *C. gorgone* (Calhoun 2003) (also see drawing 35).							
25	Blanchard	a. *Euphydryas phaeton* (Drury)	Dm,Vm	47	Dm,Vm	Blanchard	*Melitaea Phaeton*
		b. *Phyciodes batesii* (Reakirt)	Dm	47	Dm	Blanchard	*Melitaea Tharos*
		c. *Phyciodes tharos* (Drury)	Dm,Vm	47	Dm,Vm	Blanchard	*Melitaea Tharos*
NOTES: signed by Blanchard. Entire drawing was copied for Plate 47 in the same layout. The published plate identified the male *P. batesii* as a female of *P. tharos*. The figures are consistent with eastern North American phenotypes.							
26	Abbot	*Polygonia interrogationis* (Fabricius)	Dm,Vm,L,P	51	Dm,Vm,L,P	Abbot	*Vanessa C. Aureum*
NOTES: includes figure numbers to be used for B&L Plate 51, but the arrangement was ultimately changed for the final plate. There is also a penciled symbol on the drawing that was probably used to instruct the engraver to position the dorsal adult figure at an angle on the plate.							

TABLE 1. Continued

No.	Artist	Species depicted	Figures	B&L plate	Figures copied for B&L	Artist credited on B&L plate	B&L name
27	Abbot	*Junonia coenia* Hübner	Df,Vf,L,P	—	—	—	—
28	Abbot	*Junonia coenia* Hübner	Dm,Vm,L,P	49	Df,Vf,L,P	Abbot	*Vanessa Coenia*
NOTES: Scudder (1888-1889, Pl. 74, fig. 30; Pl. 83, fig. 66) copied the larva and pupa. Holland (1898, Pl. 4, fig. 66) reproduced Scudder's pupa.							
29	Abbot	*Vanessa virginiensis* (Drury)	Df,Vf,L,P	48	Df,Vf,L,P	Abbot	*Vanessa Huntera*
NOTES: drawing has a penciled reference to B&L Plate 48, as well as corresponding figure numbers and legends used on the published plate. Also includes Abbot's inscription, "*Huntera*."							
30	Abbot	*Vanessa atalanta* (L.)	Dm,Vf,L,P	—	—	—	—
NOTES: includes Abbot's inscription of "*Atalanta*."							
31	Abbot	*Nymphalis antiopa* (L.)	Dm, Vm	—	—	—	—
Notes: includes Abbot's inscription of "Antiopa." Kraus ([1964]) figured the entire drawing.							
32	Blanchard	a. *Roddia vaualbum* Denis & Schiff.	Df,Vf	50	Df,Vf	Blanchard	*Vanessa J. Album*
		b. *Polygonia progne* (Cramer)	Dm,Vm	50	Dm,Vm	Blanchard	*Vanessa Progne*
		d. *Aglais milberti* (Godart)	Dm,Vm	50	Dm,Vm	Blanchard	*Vanessa Milberti*
NOTES: signed by Blanchard. Entire drawing was copied for B&L Plate 50 in the same layout. The figures of *R. vaualbum* accompanied the original description of *V. j. album*.							
33	Abbot	*Limenitis arthemis* (Drury)	Df,Vf,L,P	53	Df,Vf,L,P	Abbot	*Nymphalis Ursula* (text), *Limenitis Ursula* (plate)
NOTES: depicts the subspecies *L. arthemis astyanax* (Fabricius). The text and plate were issued separately in B&L, accounting for the different genera used.							
34	Blanchard	*Limenitis arthemis* (Drury)	Dm,Vm,Df	54	Dm,Vm,Df	Blanchard	*Nymphalis Arthemis* (text), *Limenitis Arthemis* (plate)
NOTES: signed by Blanchard. Depicts the subspecies *L. a. arthemis* (Df) and possibly the more western subspecies *L. a. rubrofasciata* (Barnes & McDunnough) (Dm, Vm). The text and plate were issued separately in B&L, accounting for the different genera used.							
35	Abbot	*Asterocampa clyton* (B&L)	Dm,Vm,L,P	—	—	—	—
NOTES: the larva and pupa in this drawing are incorrect for this species. In his notes (Harvard), Scudder wrote, "butterfly *clyton*, but the larva & chrys. couldn't belong to it." Although the larva is not an accurate depiction of any species, Scudder (1888-1889) copied and identified it as *P. interrogationis* (Plate 74, fig. 27). He copied the pupa as that of *Polygonia comma* (Harris) (Pl. 83, fig. 39). Holland (1898, Pl. 3, fig. 27; Pl. 4, fig. 39) reproduced Scudder's figures and identifications. The same incorrect early stages were used for a drawing of this species in New Zealand (see drawing 24 for a similarly cryptic larva). The original description of *Apatura clyton* was accompanied by B&L Plate 56, which was copied from an Abbot hostplant drawing with accurate early stages							
36	Abbot	*Asterocampa celtis* (B&L)	Dm,Df,Vm,L,P	—	—	—	—
NOTES: includes Abbot's inscription, "*Portlandia*," apparently a misidentification of *Enodia portlandia* (Fabricius). In his notes (Harvard), Scudder also observed that this drawing was "marked *portlandia*." The original description of *Apatura celtis* was accompanied by B&L Plate 57, which was copied from another Abbot drawing.							
37	Duménil	*Historis odius* (Fabricius)	Dm,Vm	52	Dm,Vm	Blanchard	*Aganisthos Orion*
NOTES: includes a penciled reference to B&L Plate 52, as well as figure numbers and legends for the published plate. Although the plate credits Blanchard, a handwritten notation by Boisduval on the drawing attributes it to Duménil ("Dumenil Pinxit."). It is interesting that Boisduval used the genus *Prepona* on this drawing and referred to *Prepona* in livraison 22 of B&L, believed published in 1835. However, Boisduval is credited with authoring this genus in Boisduval (1836) (see Cowan 1969). The figures represent the continental subspecies *H. o. orion* (Fabricius), which also occurs in the Lesser Antilles.							
38	Abbot	*Libytheana carinenta* (Cramer)	Dm,Vm,L,P	—	—	—	—
NOTES: B&L Plate 64 of *Libythea motya* was copied from an Abbot hostplant drawing with duplicate early stages, but the adults were evidently derived from a specimen in Boisduval's collection (see text). Scudder (1888-1889, Pl. 84, fig. 24) copied the pupa, which was reproduced by Holland (1898, Pl. 5, fig. 24). See Figs. 29, 30.							
39	Abbot	a. *Enodia creola* (Skinner)	Dm	—	—	—	—
		b. *Enodia portlandia* (Fabricius)	Df,Vf	—	—	—	—
NOTES: Abbot incorrectly associated the male of *E. creola* with the female of *E. portlandia*. An Abbot hostplant drawing that correctly associated the male and female of *E. portlandia* was copied for B&L Plate 58.							

TABLE 1. Continued

No.	Artist	Species depicted	Figures	B&L plate	Figures copied for B&L	Artist credited on B&L plate	B&L name
40	Blanchard	*Satyrodes appalachia* (R. L. Chermock)	Dm,Df,Vm,Vf	60	Df,Vf,Dm,Vm	Blanchard	*Satyrus Canthus*
NOTES: signed by Blanchard. Entire drawing was copied for B&L Plate 60 in the same layout. *Satyrodes appalachia* was not recognized as a separate species from *Satyrodes eurydice* (Johansson) [=Satyrus canthus (L.)] until 1970. The figures represent the southeastern nominate subspecies.							
41	Abbot	a. *Hermeuptychia sosybius* (Fabricius)	Dm,Df,Vm,L,P	63	Dm,Vm,L,P	Blanchard	*Satyrus Sosybius*
		b. *Neonympha areolatus* (J. E. Smith)	Df,Vf,L,P	63	Df,Vf,L,P	Blanchard	*Satyrus Areolatus*
NOTES: Scudder (1888-1889, Pl. 83, fig. 11) copied the pupa of *N. areolatus*, which was reproduced by Holland (1898, Pl. 4, fig. 10).							
42	Abbot	a. *Achalarus lyciades* (Geyer)	Df,Vm,L,P	71	Df,Vm,L,P	Abbot	*Eudamus Lycidas*
		b. *Epargyreus clarus* (Cramer)	Dm,Vm,L,P	72	Dm,Vm,L,P	Abbot	*Eudamus Tityrus*
NOTES: includes Abbot's inscriptions, "*Lycidas*" for *A. lyciades* and "*Tytirus*" (a misspelling of the synonym *tityrus* Fabricius) for *E. clarus*.							
43	Abbot	*Urbanus proteus* (Linnaeus)	Dm,Vm,L,P	69	Dm,Vm,L,P	Abbot	*Eudamus Proteus*
NOTES: includes Abbot's inscription, "*Proteus*."							
44	Le Conte?	*Megathymus yuccae* (B&L)	larva only	—	—	—	—
NOTES: drawing is likely by J. E. Le Conte (see text). In 1876, entomologist Charles V. Riley published the life history of this species. In Scudder's notes (Harvard) there is a sketch of this figure, which Scudder later sent to Riley and asked, "is this *Megathymus yuccae*?", to which Riley replied, "without doubt!" *Eudamus yuccae* was first "described" (no textual reference) from an Abbot hostplant drawing on B&L Plate 70.							
45	Blanchard	a. *Calpodes ethlius* (Stoll)	Dm,Vm	75	Dm,Vm	Blanchard	*Eudamus? Olynthus*
		b. *Polites vibex* (Geyer)	Df(2),Vf	75	Df(2),Vf	Blanchard	*Hesperia Brettus*
NOTES: signed by Blanchard. Entire drawing was copied in the same layout for B&L Plate 75, which included the original "descriptions" (no textual references) of *E. olynthus* and *H. brettus*. Boisduval apparently considered the sexes of *P. vibex* to be analogous, as figures 3 & 4 of dorsal and ventral females were both identified as males on B&L Plate 75.							
46	Abbot	*Problema bulenta* (B&L)	Dm,Df,Vm,L,P	67	Dm,Df,Vm,L,P	Abbot	*Hesperia Bulenta*
NOTES: figures copied for B&L Plate 67, the original "description" (no textual reference) of *H. bulenta*. In his notes for another drawing of *P. bulenta* in New Zealand, Abbot wrote, "Feeds on the Broad grass, *Zozani aquatica* folding itself up in the leaf changed 25th bred 6th Aug't. Frequents Rice fields, ditches, and the sides of ponds in the lower parts of Georgia is not common." The species was not rediscovered until 1925. Abbot probably collected his specimens near the mouth of the Savannah River where the species still occurs today.							
47	Abbot	a. *Hylephila phyleus* (Drury)	Dm,Df,Vm,L,P	78	Dm,Df,Vm,L,P	Abbot	*Hesperia Phyleus*
		b. *Wallengrenia otho* (J. E. Smith)	Dm,Df,Vm,L,P	77	Dm,Df,Vm,L,P	Abbot	*Hesperia Otho*
NOTES: Scudder (1888-1889, Pl. 77, figs. 19, 34; Pl. 85, figs. 39, 42) copied all the larvae and pupae. The pupae were reproduced by Holland (1898, Pl. 6, figs. 39, 42).							
48	Blanchard	a. *Wallengrenia egeremet* (Scudder)	Dm,Df	—	—	—	—
		b. *Wallengrenia otho* (J. E. Smith)	Vf	—	—	—	—
		c. *Poanes zabulon* (B&L)	Df,Vf	—	—	—	—
		d. *Amblyscirtes aesculapias* (Fabricius)	Dm,Vm	—	—	—	—
NOTES: signed by Blanchard. Drawing predates the description of *W. egeremet*, which until recently was generally treated as conspecific with *W. otho*. A penciled circle around the *Wallengrenia* figures and the notation "remplacer" [replace] suggests that Boisduval was going to copy them for B&L, but instead used those from Abbot's drawing 47.							
49	Blanchard	a. *Nastra lherminier* (Latrielle)	Df	—	—	—	—
		b. *Polites origenes* (Fabricius)	Df	—	—	—	—
		c. *Polites themistocles* (Latrielle)	Vf	—	—	—	—
		d. *Atalopedes campestris* (Boisduval)	Dm,Vm	—	—	—	—
		e. *Poanes yehl* (Skinner)	Dm,Vm	—	—	—	—
NOTES: signed by Blanchard. Females of up to three different species are associated in this drawing (probably Boisduval's misidentification). The second dorsal female may represent *P. themistocles*, but it cannot be identified with certainty. The figures of *A. campestris* represent the subspecies *A. c. huron* (W. H. Edwards).							
50	Blanchard	a. *Anatrytone logan* (W. H. Edwards)	Dm,Df,Vf	-	-	-	-
		b. *Polites peckius* (W. Kirby)	Dm,Vm	-	-	-	-
NOTES: signed by Blanchard. The figures of *A. logan* are consistent with the nominate subspecies from eastern North America.							

TABLE 1. Continued

No.	Artist	Species depicted	Figures	B&L plate	Figures copied for B&L	Artist credited on B&L plate	B&L name
51	Blanchard	a. *Polites themistocles* (Latreille)	Dm,Vm	76	Dm,Vm	Blanchard	*Hesperia Cernes*
		b. *Atrytone arogos* (B&L)	Dm,Df,Vm	76	Dm,Df,Vm	Blanchard	*Hesperia Arogos*
		c. *Poanes zabulon* (B&L)	Dm,Vm	76	Dm,Vm	Blanchard	*Hesperia Zabulon*
NOTES: signed by Blanchard. Entire drawing copied for Plate 76 in the same layout and used for the original "descriptions" (no textual references) of *H. cernes*, *H. arogos* and *H. zabulon*. See Fig. 5. The figures of *A. arogos* represent the nominate subspecies from eastern North America.							
52	Blanchard	a. *Polites baracoa* (Lucas)	Dm,Vm	—	—	—	—
		b. *Wallengrenia ophites* Mabille	Dm,Vm	—	—	—	—
NOTES: drawing depicts two West Indian species. The *P. baracoa* figures may represent the Hispaniolan subspecies *P. b. loma* Evans.							
53	Blanchard	a. *Euphyes vestris* (Boisduval)	Dm,Df,Vf	—	—	—	—
		b. *Lerema accius* (J. E. Smith)	Dm,Df,Vf	—	—	—	—
		c. *Oligoria maculata* (W. H. Edwards)	Dm,Vm	—	—	—	—
NOTES: signed by Blanchard. Illegible notations, scrawled in Boisduval's hand, are partially cut off in the right margin. The figures of *E. vestris* are consistent with the eastern North American subspecies *E. v. metacomet* (Harris).							
54	Blanchard	a. *Panoquina ocola* (W. H. Edwards)	Dm,Df,Vm	—	—	—	—
		d. *Pholisora catullus* (Fabricius)	Dm,Df,Vm	—	—	—	—
NOTES: signed by Blanchard.							
55	Abbot	a. *Erynnis brizo* (B&L)	Dm,Df,Vm,L,P	—	—	—	—
		b. *Erynnis juvenalis* (Fabricius)	Dm, Df, Vm	65	Dm, Df, Vm	Abbot	*Thanaos Juuvenalis*
NOTES: includes Abbot's inscription, "*Juvenalis*" (for E. juvenalis). The identities of the sexes of the dorsal figures of *E. juvenalis* were reversed on B&L Plate 65. *Thanaos brizo* was originally "described" (no textual reference) from B&L Plate 66, which was copied from an Abbot host plant drawing with duplicate figures and a hostplant. A penciled circle drawn around the figures of *E. brizo* suggests Boisduval was going to copy them for B&L, but instead used the other Abbot drawing. Scudder (1888-1889, Pl. 77, fig. 18; Pl. 85, fig. 38) copied the larva and pupa of *E. brizo*, which were reproduced by Holland (1898, Pl. 6, fig. 38).							

drawings at the University of South Carolina depict butterflies. Forty include figures that were reproduced on 44 of the 78 plates in Boisduval & Le Conte (1829-[1837]), hereafter referred to as B&L. The butterfly determinations and information about the corresponding published plates are presented in Table 1. Nomenclature follows Opler & Warren (2002). The butterfly drawings portray at total of 80 species and most include multiple species (Figs. 3-5, 10, 36). The 94 moth drawings in this set are still under review.

The drawings at the University of South Carolina were rendered on cream-colored wove paper and measure approximately 27 cm x 16.5 cm. They are mounted on stiff paper backing, matted, and contained in six blue half-morocco portfolio cases with gilt lettering that incorrectly identify them as the original drawings for Smith & Abbot (1797) (Figs. 1, 2). The portfolio cases were created by rare book firm H. P. Kraus of New York, who sold the drawings to the University of South Carolina in 1964 (Calhoun 2003). The drawings by John Abbot were rendered in a horizontal format, with figures of early stages positioned above the adults (Figs. 2, 3, 4, 10, 36). When J. E. Le Conte commissioned Abbot for these drawings in 1813, he requested that hostplants be omitted (Rogers-Price 1983). The drawings by Blanchard and Duménil were mostly rendered in a vertical format, do not include early stages, and depict only one half of dorsal adults. Nearly all of Blanchard's drawings have a penciled outline around the figures and are signed, "E. Blanchard, pit." (Figs. 5, 5a). Blanchard's artistic style was highly refined and true to life. Although Abbot's figures were rearranged for the plates in B&L, virtually all of the published drawings by Blanchard and Duménil were reproduced in their original layouts.

One drawing in this set portrays only the mature larva of *Megathymus yuccae* (Boisduval & Le Conte) with copious annotations in Latin and French by J. E. Le Conte (Table 1). It was drawn on a smaller piece of paper that was pasted onto a larger sheet. The style of this drawing is similar to smaller drawings of moth larvae in this set, most of which were probably rendered by Le Conte (Calhoun 2003). This is supported by the notes of John Abbot, who credited Le Conte (as "Mr. Le Compt") for discovering the larva of *M. yuccae*. In Boisduval et al. (1832-1837), Boisduval wrote about caterpillar drawings that he had received from New York and Savannah, obviously referring to Le Conte (from New York) and Abbot (who lived for a time in Savannah, Georgia). Boisduval

FIGS. 1-2. Portfolio cases of original drawings in the Thomas Cooper Library, University of South Carolina. 1, Five of the six cases. 2, Case 1 opened to show the matted illustrations (Abbot's drawing 2 of *E. marcellus* is visible). (photos courtesy of Thomas Cooper Library)

(1836) also noted that Le Conte had executed as many caterpillar drawings as Abbot.

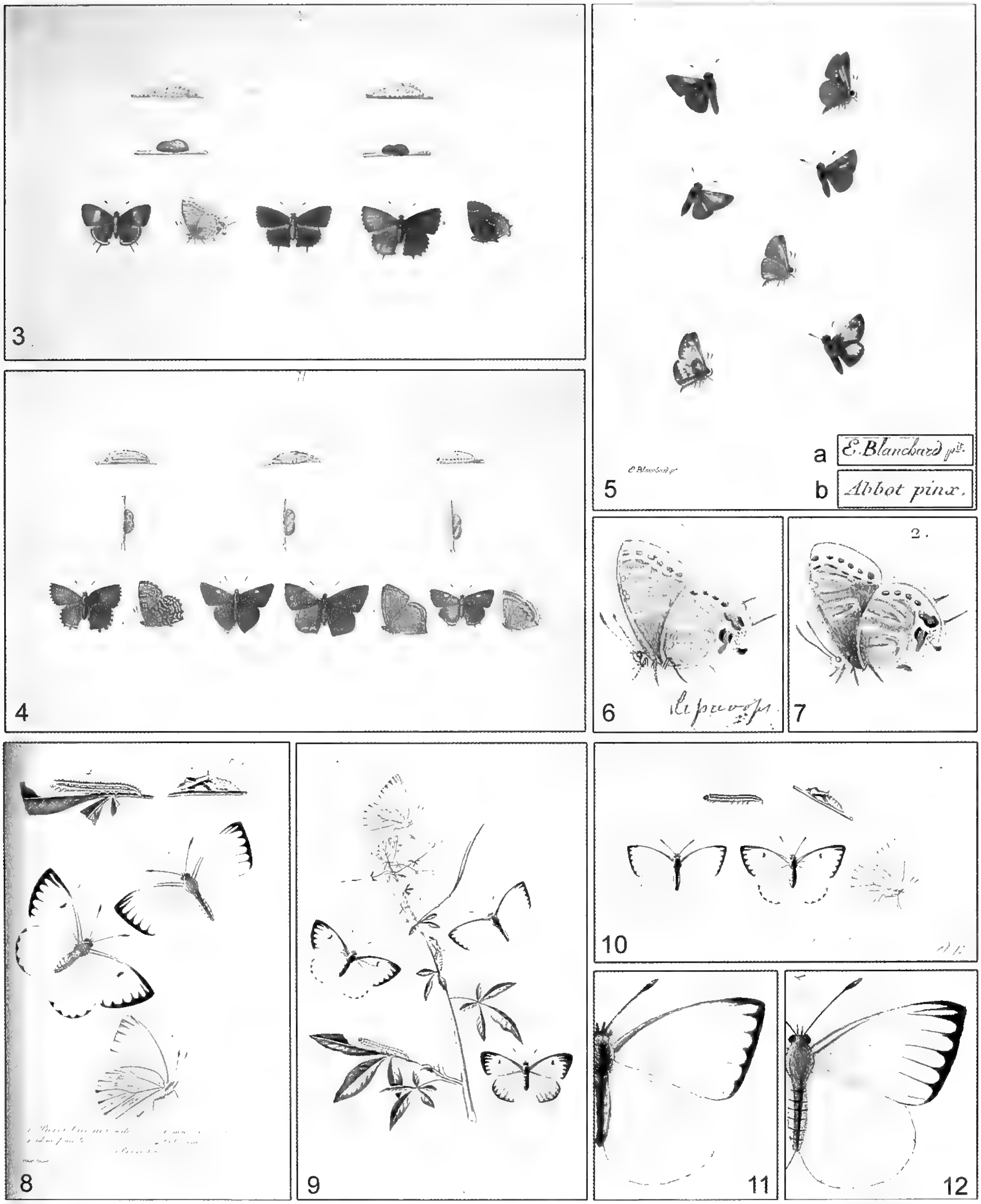
The drawings at the University of South Carolina are numbered in pencil and loosely arranged in taxonomic order. Most have notations that were written by Boisduval and/or Le Conte, including names used in B&L. Although I previously suspected that the majority of the inscriptions on these drawings were by Boisduval (Calhoun 2003), I have since confirmed through additional writing samples that Le Conte was responsible for many names and other notations (Fig. 6). Samuel H. Scudder examined these drawings while they were still in Boisduval's possession and also observed that, "in some of Abbot's drawings which Dr. Boisduval received from Major LeConte is a memorandum by the latter" (Scudder 1888-1889). "Nobis," or more often the abbreviation "nob.," follows many of the species names. This Latin term loosely means "of us" or "of me" and was used to claim authorship of new names. Ten of the drawings possess penciled references to the corresponding B&L plates ("planches" in French) (e.g., "Pl. 1") (Table 1, Fig. 10). Some individual figures are numbered (Fig. 6) and three drawings even include the complete figure legends used on the published plates. On several drawings, Abbot inscribed the same Latin names employed in Smith & Abbot (1797). The source of other inscriptions is not readily identifiable.

Many of the drawings by Abbot that were copied for published plates show alterations, particularly to the legs and bodies of adults. Referring to this set of drawings, Oberthür (1920) complained that Abbot's legs and bodies were more fantasy than reality. In the preface to B&L livraison 10, Boisduval addressed criticisms from subscribers about the inaccuracy of various published figures, particularly relating to poorly formed bodies and legs. In a statement under the heading "Avis de L'un des Auteurs" [Opinion of One of the Authors], Boisduval promised to retouch Abbot's drawings and that beginning with livraison 10 the published figures would no longer exhibit these defects (an imprecise translation in Calhoun (2003) suggested the engravings were altered). The retouched drawings in South Carolina were used for plates issued after livraison 10, further supporting this connection. The style of the alterations closely matches that of Blanchard, who was probably instructed by Boisduval to improve and standardize the figures for the engravers.

When S. H. Scudder visited Boisduval, probably in 1871, he sketched at least 23 of Abbot's larvae and pupae in these drawings. Scudder (1888-1889) published these facsimiles, some of which were later reproduced by Holland (1898) and Klots (1951) (Table 1). The auction catalog of Sotheby & Co. (1963) figured an entire moth drawing from this set (no. 106). Kraus ([1964]) and Rogers-Price (1983) figured five butterfly drawings (nos. 31 and 3, 16, 18, 21, respectively).

Missing drawings. Published Plates 4-11, 19, and 20 were copied from missing Abbot drawings that were probably rendered in the same format as those in South Carolina. Oberthür (1920) also feared that several original drawings from this set were lost. One such drawing, depicting *Eurema lisa* Boisduval & Le Conte, was used for B&L Plate 19 and apparently also for figures of the early stages of this species in Boisduval (1836, Pl. 2).

There are fifteen plates from Abbot in B&L that included sizable hostplants (nos. 32, 37, 55-59, 61, 62,



FIGS. 3-12. Original drawings and published plates. B&L = Boisduval & Le Conte (1829-[1837]). **3**, John Abbot's drawing 3° of *S. liparops* and *C. henrici*. **4,** Abbot's drawing 11° of *C. niphon*, *S. titus*, and *C. gryneus*. **5**, Blanchard's drawing 51° of *P. themistocles*, *A. arogos*, and *P. zabulon* used for B&L Plate 76. **5a**, Blanchard's signature. **5b**, Notation crediting Abbot for B&L Plate 64. **6,** Ventral *S. liparops* from Abbot's drawing 12° (note "2" above figure); inset is *"liparops"* in Le Conte's hand. **7,** Ventral female of *Thecla liparops*, B&L Plate 31, fig. 2. **8,** B&L Plate 16 of *Pieris cleomes*. **9,** Abbot's drawing of *A. m. phileta*, New Zealand (ref. no. E-272-f-012). **10,** Abbot's drawing 7° of *A. m. phileta* (reference to "Pl. 16" at lower right) **11,** Dorsal male from Abbot's drawing 7° of *A. m. phileta*. **12**, Dorsal male of *P. cleomes*, B&L Plate 16. (° Thomas Cooper Library, University of South Carolina)

64, 66, 68, 70, 73, 74) (Fig. 24). The original drawings for these plates are also missing, but Scudder (1888, 1888-1889) noted that he obtained from Boisduval "three series of manuscript notes entitled 'Notes to the Drawings of Insects,' all written in Abbot's own hand, and comprising twenty-seven foolscap pages, rather closely written, and describing the changes of two hundred and one species; of these thirty-eight are butterflies." Scudder donated these notes in 1903 to the Boston Society of Natural History. In 1946, Harvard University obtained them as part of a larger acquisition that also included approximately 600 original Abbot drawings owned by the Society. I obtained a copy of these notes, which are now deposited in the Houghton Library. The thee sets of notes were segregated by Abbot as "a," "b," and "c." Written on the cover sheet in Scudder's hand is "Given me by Dr. Boisduval SHS." These notes include entries that correspond to species portrayed with hostplants in B&L. Abbot must have presented these drawings to Le Conte, who then passed them to Boisduval along with Abbot's drawings now in South Carolina.

These missing hostplant drawings (depicting both insects and hostplants) probably also account for abbreviated plants found in other plates in B&L. Plates 16, 18, 22, 25-30 included hostplant leaves or small sprigs, which served as substrates for figures of larvae and pupae (Figs. 8, 15). P. Duménil was the master engraver for the first 30 plates in B&L, including the nine with abbreviated hostplants. He apparently created two of these (nos. 16, 22) by combining Abbot's figures in South Carolina with portions of plants from Abbot's missing hostplant drawings. Penciled references to these two published plates are found on drawings in South Carolina (nos. 7, 9) and the plants match those in other surviving Abbot drawings. For four of the remaining seven plates that have no equivalent drawings in South Carolina (nos. 18, 25, 28, 29), Duménil must have derived the illustrations from the missing hostplant drawings, but reproduced only fragments of the plants to remain consistent with his other plates. The plant in Plate 30 (Fig. 15) appears to have been copied from an illustration in Smith & Abbot (1797) (see Discussion). It was not until Duménil was replaced by another engraver, known simply as Borromée, that Abbot's hostplant drawings were reproduced in their entirety. Whereas Duménil and his association with Boisduval are fairly well understood (see Cowan 1969),

TABLE 2. Entries from John Abbot's notes (Harvard University) that correspond to hostplant plates in Boisduval & Le Conte (1829-[1837]) (= B&L). Grammar and spelling are as given in the original notes. Asterisks (*) denote entries that were assigned to plates from limited information.

B&L plate	Species depicted	Set and entry number	Notation
16	*Ascia monuste* (L.)	b.6	"White Butterfly. Danai Cleome. Feeds on the *Cleome pentaphilles*. changed 17th July, bred 23rd July. nearly half of the female Butterflies varies being of a Dingy colour, as figured, They are generally rare, but some years at intervals are very plenty in the lower parts of the County, I am indebted for the discovery of the caterpillar of this Species to my friend Mr. Oemler, who first found it in his garden in Savannah."
18	*Eurema daira* (Godart)	b.8	"Black streaked little yellow Butterfly. Feeds on the *Cassia Arameicrista*, Tyed itself up 27th Aug't changed 28th bred 5th Sep'r. Both these kinds [this and *Eurema lisa* Boisd. & Le Conte; prior entry in notes] is common in all parts of the County in Autumn, and settles so many together at times to suck moist places on the ground, that I have seen 20 in the compass of a hat."
22	*Zerene cesonia* (Stoll)	a.30	"Clouded yellow Butterfly. Feeds on the Plant figured. Tyed up 18th April, changed 19th bred 2nd May, continues to breed all the Summer and Autumn, Is most common in the pine woods, often settles several together to suck the moist places in roads, and other places."
25	*Atlides halesus* (Cramer)	c.7	"Great Purple hair Streak. Feeds on the Willow Oak, *Quercus phellos*. Tyed itself up 18th Aug't changed 20th bred 6th Sep'r is not common."

TABLE 2. Continued

B&L plate	Species depicted	Set and entry number	Notation
28	*Strymon melinus* (Hübner)	c.8	"Red spotted hair streak Butterfly. Feeds on the Flower figured, Parsley Haw, pine, Snap beans etc. Tyed itself up 28th April, changed 20th bred 14th May. Is not very common."
29	*Satyrium calanus* (Hübner)	b.17	"Black hair streak Butterfly. Feeds on the Parsley Haw, and Oaks and Hickory. Tyed up 25th April, changed the 28th bred 10th May. The Butterfly frequents Chinquepin blossoms and is not uncommon in the oak woods."
32	*Callophrys irus* (Godart)	c.9°	"Little Brown Butterfly. Feeds on the plant figured etc. Tyed up 20th June, changed 22nd bred 20th March. is very rare."
37	*Feniseca tarquinius* (Fabricius)	a.37	"Orange Butterfly. Feeds on the Wild Currant Tree, and Alder, the Caterpillar is partly covered with a white loose down, Tyed up 12th April, changed 14th bred 25th. The Butterfly frequents Swamps. is rare."
55	*Limenitis archippus* (Cramer)	a.25, c.2	"Black veined orange Butterfly. Feeds on Willow. Tyed up 30th July, changed the 31st bred 7th August. neither the Caterpillar or Butterfly is very common, most frequent near Savannah" [a.25]. "Black veined Orange Butterfly. Feeds on the Plant figured; and Willow mostly. Tyed up 30th July, changed into Chrysalis the 31st bred 7th August. Is not very common" [c.2; this is probably the entry for the drawing used by B&L].
56	*Asterocampa clyton* (Boisduval & Le Conte)	a.27°	"Orange brown Butterfly. Feeds on the plant figured, Tyed up 16th May changed 17th bred 2nd June. Is a rare species" [°common name is comparable to "Orange coloured Butterfly" for *A. clyton* drawing in New Zealand; the dates are also similar].
57	*Asterocampa celtis* (Boisduval & Le Conte)	a.29	"Sugar berry Butterfly. Feeds on the Sugar berry (or Hack berry), Tyed up 23rd May, changed 24th , bred 12 June. Is a rare Species."
58	*Enodia portlandia* (Fabricius)	a.31°	"Reed Butterfly. Feeds on Reeds, Tyed up 16 June, changed 17th bred 25th mostly frequents Swamps in different parts of the County, but is not a common species."
59	*Cercyonis pegala* (Fabricius)	b.9	"Great Meadow brown Butterfly. Feeds on the grass figured, and other grasses. Tyed up 19th June changed 20th bred 5th July. Frequents the pine woods etc. is not common."
61	*Megisto cymela* (Cramer)	a.32°	"Ringlet Butterfly. Feeds on the grass figured, and other grasses. Tyed up 25[4]th April, changed 24[5]th bred 2nd May. Is plenty in Hammocks and the side of Branches, in most parts of the country" [° This entry does not refer to *Hermeuptychia sosybius* (Fabricius), as entry b.10 is identical to notes for a drawing of this species in New Zealand].
62	*Cyllopsis gemma* (Hübner)	c.6°	"Swamp Butterfly. Feeds on the grass figured, and other grasses. Tyed up 10th April, changed 11th bred 24th. frequents Swamps and Hammocks is not common."
64	*Libytheana carinenta* (Cramer)	b.11	"Snout Butterfly. Feeds on the Sugar berry, or Hack berry, Tyed up 28th April changed 29th bred 8th May. Is rare."
66	*Erynnis brizo* (Boisduval & Le Conte)	a.33	"Lesser Dingy Skipper. Feeds on the Vine figured, Wild Indigo, and Oaks, spun up last Oct, changed into Chrysalis in March, bred 21st April, Is not so common as the larger kind."

TABLE 2. Continued

B&L plate	Species depicted	Set and entry number	Notation
68	*Euphyes arpa* (Boisduval & Le Conte)	c.4°	"Georgia Skipper Butterfly. Feeds on the grass figured, and other grasses, Spun up 25th April, Frequents the sides of Ponds in the pine Woods, is rare" [dates and habitat are consistent with *E. arpa*; hostplant on the B&L plate is giant whitetop, *Rhynchospora latifolia* (Baldwin) W. W. Thomas (Cyperaceae)-a "grass" to Abbot. This skipper normally feeds on saw palmetto, *Serenoa repens* (Bartr.) Small (Palmae), but Minno (1994) reared it in the lab on a species of Cyperaceae, suggesting Abbot could also have reared it on the sedge. Abbot may have considered *E. arpa* and *Euphyes pilatka* (W. H. Edwards), which feeds on *Cladium jamaicense* Crantz (Cyperaceae), to be the same species. Nonetheless, the adults and pattern on the head capsule of the larva in the published plate are consistent with *E. arpa*].
70	*Megathymus yuccae* (Boisduval & Le Conte)	a.45	"Great Georgia Skipper Butterfly. Lives and feeds on the heart and bud of the Bear grass or Wild Aloe, closing the top together with a web, and in which its changes into Chrysalis, one which changed the 17th May, was bred the 20th June. Those that changes in Autumn lives in Chrysalis in the Aloe all winter, coming out the last of March & April, is rare but most frequent in the lower parts of the County. I am indebted to Mr. Le Compte for the discovery of the Caterpillar and manner of living of this rare and elegant Species. The Chrysalis is covered with a kind of powder similar to the Underwing Moths." [the dorsal female on B&L Plate 70 represents *Megathymus cofaqui* (Strecker)].
73	*Autochton cellus* (Boisduval & Le Conte)	c.3	"Barr'd Skipper Butterfly. Feeds on the Convolvulus figured, spun up 4th April, bred 25th . Frequents the sides of Swamps, is rare."
74	*Thorybes bathyllus* (J. E. Smith)	b.12	"Brown Skipper. Feeds on the Beggers lice, spun up in the leaves 18th Oct'r bred 20th April, is not very common."

Borromée is obscure. Even his full name is unknown. He was an Italian artist and engraver active in France during the first half of the 19th century and worked as a natural history illustrator for the Muséum National d'Histoire Naturelle in Paris where some of his artwork is currently deposited (Meissner 1996). Borromée also served as the master engraver for Boisduval (1836).

I compared the three sets of Abbot's notes at Harvard with other notes that he prepared for his drawings now in London (Scudder 1872, 1888-1889) and New Zealand, and have identified entries for 21 of the 24 missing hostplant drawings used for plates in B&L (Table 2). Two of these drawings were copied for plates that accompanied the original descriptions of *Apatura clyton* Boisduval & Le Conte (= *Asterocampa clyton*) (Plate 56) and *Apatura celtis* Boisduval & Le Conte (= Asterocampa celtis) (Plate 57). Four drawings were copied for plates that represent the "original descriptions" (no accompanying text) of *Thanaos brizo* Boisduval & Le Conte (= *Erynnis brizo*) (Plate 66), *Hesperia arpa* Boisduval & Le Conte (= *Euphyes arpa*) (Plate 68), *Eudamus yuccae* Boisduval & Le Conte (= *Megathymus yuccae*) (Plate 70), and *Eudamus cellus* Boisduval & Le Conte (= *Autochton cellus*) (Plate 73). Abbot's accompanying notes help to fill the void where no text was provided for these published plates.

The host leaves in Plates 26 and 27 are unaccounted for. Ironically, both plates portray *Parhassius m-album* Boisduval & Le Conte and do not have corresponding entries among Abbot's notes at Harvard. The figures of *P. m-album* on drawing 10 in South Carolina are numbered, indicating that all the figures on Plate 27 were copied from this rendering. The leaf on this plate is crude and looks to have been created by Duménil merely to improve composition. There is also no appropriate entry for Plate 30 that combined figures of two species under the name of *Thecla favonius* (J. E. Smith) (see Discussion). By comparing notes from surviving sets of Abbot drawings, I verified that the remaining butterfly entries refer to species not treated in B&L.

Artists responsible for the published plates. The plates in B&L included small printed notations that credited the original drawings to Abbot, Blanchard, Duménil, or Le Conte (Fig. 5b). Following the name of each artist was printed "pinx." or "pinxit," from the Latin meaning "painted by." Based on these notations, Rogers-Price (1983) attributed 62 plates to Abbot, whereas Gilbert (1998) listed 65. dos Passos (1962) seemingly misunderstood the notations, believing 62 plates were merely "coloured by Abbot." I examined the plates from the copy of B&L once owned by dos Passos (Wittenberg University, Ohio) and confirmed that 62 plates credited Abbot (nos. 1-20, 22, 24-29, 31-34, 36, 37, 39, 40, 42, 44, 46, 48, 49, 51, 53, 55-59, 61, 62, 64-74, 77, 78). Twelve plates credited Blanchard (nos. 35, 38, 41, 45, 47, 50, 52, 54, 60, 63, 75, 76), three credited Duménil (nos. 21, 23, 30), and one credited Le Conte (no. 43). For Plates 1-8 and 10-30 Duménil misspelled Abbot as "Abbott." With the exception of Plates 36 and 37 where "Obbit" was given, Borromée spelled the name correctly (Table 1).

As demonstrated by the drawings in South Carolina, as well as other original and published illustrations by Abbot, the wrong artist was credited on seven plates (nos. 3, 14, 15, 17, 43, 52, 63) (Table 1). Fifty-seven plates can be wholly attributed to Abbot (nos. 1, 2, 4-13, 16, 18-20, 22, 24-29, 31-33, 36, 39, 40, 42-44, 46, 48, 49, 51, 53, 55-59, 61-63, 65-74, 77, 78). Two plates from Abbot (nos. 34, 37) also included figures from Blanchard. Two plates (nos. 30, 64) were largely derived from Abbot, but included adult figures that were evidently derived from specimens in Boisduval's collection (see Discussion). Ten plates were from Blanchard (nos. 35, 38, 41, 45, 47, 50, 54, 60, 75, 76). Seven plates were most likely from Duménil (nos. 3, 14, 15, 17, 21, 23, 52).

DISCUSSION

The origin of figured specimens. Figures for nine of the 29 original descriptions in B&L were from drawings by Émile Blanchard (Table 1). This finding complicates historical notions about the type localities of five taxa: *Eudamus olynthus* Boisduval & Le Conte, *Hesperia brettus* Boisduval & Le Conte, *Hesperia cernes* Boisduval & Le Conte, *Hesperia arogos* Boisduval & Le Conte, and *Hesperia zabulon* Boisduval & Le Conte. No text accompanied Plates 75 and 76, but based on the belief that the published figures were from John Abbot, Bell (1938) and Miller & Brown (1981) assigned these taxa the type locality of "Georgia." Such assumptions are no longer appropriate.

Abbot usually drew insect specimens that he reared and collected himself, but he occasionally illustrated specimens obtained from other local naturalists, particularly pharmacist Augustus G. Oemler of Savannah, Georgia, and botanist Stephen Elliott of South Carolina. Abbot provided many plant specimens for Elliott's herbarium and exchanged a set of insect watercolors for specimens that Elliott had personally obtained in Georgia and South Carolina (Rogers-Price 1983, Gilbert 1998). Specimens collected by Abbot were dispersed to many European naturalists during the late 18th and early 19th centuries, mostly through London jeweler John Francillon. Swainson (1840) observed that Abbot's insects "were always sent home expanded, even the most minute." At least some specimens were labeled "Georgia" in Abbot's own hand (Calhoun 2003). Many of these specimens found their way into various museums, but it is impossible to know if any were used as models for his drawings.

On the other hand, Blanchard and Duménil undoubtedly drew specimens contained in the extensive collection of Boisduval, who obtained them from multiple sources. Boisduval (1836) wrote that he had received from Le Conte an immense quantity of species from North America. In turn, some specimens that Le Conte gave to Boisduval came from Thaddeus W. Harris (Scudder 1869) and Abbot. In B&L, Boisduval noted that a specimen "nous a eté envoye par Abbot" [has been sent to us by Abbot]. Harris also had specimens from Abbot, now deposited in the Museum of Comparative Zoology, Harvard University. Boisduval possessed Abbot specimens, but it may be difficult to establish that Blanchard and Duménil used any of them as subjects for their drawings. Six unused drawings by Blanchard in South Carolina (nos. 48, 49, 50, 52, 53, 54) were probably prepared for the planned continuation of B&L. To better understand the origin of figured specimens in Blanchard's drawings, I have identified the applicable subspecies in Table 1 where possible.

Four plates attributed to John Abbot in B&L portrayed butterflies that he certainly never encountered in Virginia or Georgia. Harris (1972) wondered how Abbot was able to obtain specimens of these exotic species. Unfortunately, only one of the original drawings for these plates is included in the set in South Carolina. Three plates portray West Indian species: *Eurytides celadon* (Lucas) (as *Papilio sinon*, Pl. 3), *Battus devilliersii* (Godart) (as *Papilio villersii*, Pl. 14), and *Battus polydamas* (L.) (as *Papilio polydamas*, Pl. 15). The text did not mention Virginia or Georgia within the ranges of these species. Although *B. polydamas* is a resident of Florida that occasionally strays into Georgia (Harris 1972), and Boisduval (1836) dubiously stated that the species was very common in Georgia, the plate in B&L actually depicted the distinctive subspecies *B. p. neodamas* (Lucas) that occurs only on the Lesser Antilles islands of Guadeloupe and Marie-Galante. These islands were under French control during most of the late 18th and early 19th centuries. The most unusual species treated in B&L is the Asian *Leptosia nina* (Fabricius) (as *Pieris chlorographa*) (Plate 17, figs. 4, 5). Boisduval hesitantly included this butterfly, as he was uncertain that the two specimens he possessed actually came from North America. He soon rectified this error, admitting "C'est par erreur, et sur la foi d'Hubner, que nous avons figuré cette variété dans notre Iconographie…nous avons maintenant la certitude qu'elle vient de I'lle de Java" [it is by mistake, and on the faith of Hübner, that we have figured this variety in our Iconography…we are now certain that it comes from the island of Java] (Boisduval 1836). Obviously, Abbot did not collect the figured specimens, nor have I found evidence that he received such specimens to illustrate from Boisduval, Le Conte, or anyone else. Although Abbot obtained specimens from New England during his residency in America (Remington 1948), it does not appear that he ever drew Lepidoptera that originated from anywhere outside the region extending from Virginia to Georgia.

In all probability, these four plates that included extralimital species were created entirely by Duménil, who engraved five of the six plates in B&L that included Neotropical and Asian species (Pls. 3, 14, 15, 17, 23). He was also credited as the artist for Plate 23 of *Anteos maerula* (Fabricius). Although Borromée engraved the sixth plate, *Historis odius* (Fabricius) (Pl. 52), it was based on drawing 37 in South Carolina that Boisduval attributed to Duménil (Table 1). Drawing 4 in South Carolina of *E. celadon* (for Plate 3) is probably also by Duménil (Table 1). All six plates that included tropical species should tentatively be credited to Duménil. Because only two drawings for these plates survive, Duménil may have engraved the remaining three plates directly from Boisduval's specimens. The same can be said for Plate 21 that included figures for the original description of *Colias pelidne* Boisduval & Le Conte. This plate credited Duménil as the artist and no corresponding original figures are included among the drawings in South Carolina. Boisduval (1836) noted specimens of this species in his personal collection at the time the plate was created. Duménil also provided the original drawings and served as the master engraver for many of the plates in Dejean & Boisduval (1829-1837) and Boisduval et al. (1832-1837).

The figures for the original description of *Pieris protodice* Boisduval & Le Conte (= *Pontia protodice*) (Plate 17, figs 1-3) were portrayed on the same plate as *L. nina* and credited to Abbot. However, the text referred to the occurrence of this species only in New York and Connecticut. Boisduval (1836) again placed this species further north when he stated that it had been found in the vicinity of New York and Philadelphia. A drawing in The Natural History Museum, London, reveals that Abbot also encountered this species in Georgia, but he considered it "very rare" and noted only a single capture on 13 May. This drawing depicts the dorsal and ventral surfaces of a single female, rather than a dorsal male, dorsal female, and ventral female as portrayed on the B&L plate. The dorsal figures on the plate were also engraved with disproportionately small hindwings, an unlikely result if they had been copied from an Abbot drawing. Like the figures of *L. nina* on the same plate, Duménil probably derived those of *P. protodice* from specimens in Boisduval's collection.

Miller & Brown (1981) were unaware of a supposed type of *P. protodice*, but a male of this species was discovered in the NMNH among specimens recognized as Boisduval types acquired via the William Barnes collection. The printed labels read "EX-MUSAEO/Dris. [Doctoris] BOISDUVAL" and "Oberthur Collection." The handwritten determination label reads "Protodice. B. Sp./Am: Sept:." A red-bordered label reads "Type/protodice/a/c Höfer." The determination label is similar in format to labels by Boisduval, but is not in Boisduval's hand. It may have been written by Louis M. A. Depuiset, who helped maintain Boisduval's insect collection (Clément 1887). The abbreviation "B. Sp." probably refers to "Boisduval [as treated in] Species Générale" [Boisduval 1836]. The locality, "Am: Sept:" refers to Amérique Septentrionale [northern (North) America]. Boisduval (1836) confirmed that his collection contained specimens of *P. protodice* around the time when B&L Plate 17 was prepared. The specimen in the NMNH may further support the theory that the published figures were derived, not from a drawing by John Abbot, but from specimens in Boisduval's collection. Rather than "probably Screven Co., Georgia" as proposed by Miller & Brown (1981), the type locality of *P. protodice* is hereby amended to New York. J. E. Le Conte lived in New York and conceivably collected the figured specimens, including the "type" in the

NMNH.

Boisduval type specimens. Remarks are necessary regarding the Boisduval type specimens of North American Lepidoptera. In 1876, three years prior to his death, Boisduval bequeathed his Lepidoptera collection to Charles M. Oberthür of Rennes, France (Oberthür 1880). In 1913, American lepidopterist William Barnes organized a project for the purpose of comparing North American Lepidoptera specimens against the types in European museums (Barnes & McDunnough 1914, Oberthür 1913, 1914). The actual work was conducted by Barnes' curator, James H. McDunnough, who visited Oberthür on 13-14 October 1913 to examine the Boisduval material. Because Boisduval had designated very few type specimens, McDunnough and Oberthür personally selected Boisduval specimens to serve as types (Oberthür 1913, 1914). Oberthür (1913, 1914, 1920) figured many of these specimens, chiefly those from California described in Boisduval (1852, 1869). This selection process was largely based on existing determination labels and resulted in some misidentified "types" (Brown 1965, see Discussion).

Upon Oberthür's death in 1924, his collection was sold for the benefit of his heirs. Appointed to organize the sale was Carl Höfer (Riley 1927), who may have been Oberthür's curator (Emmel et al. 1998). Nothing further is known of Höfer; even the exhaustive historical files of the library of the Deutsches Entomologisches Institut, Eberswalde, Germany, lack information about his identity (R. Gaedike, pers com.). With the exception of the Sphingidae and Hesperiidae, William Barnes purchased the Boisduval "types" of North American Lepidoptera (Riley 1927, Horn et al. 1990). According to information on some of the specimen labels (Fig. 14), Barnes received this material in 1925. Oberthür's brother, René, purchased the specimens of Hesperiidae. In late 1926 and early 1927, the bulk of the C. Oberthür collection, about 750,000 specimens, was secured by the British Museum (N. H.) (now The Natural History Museum, London) (Riley 1927, 1964). The specimens of Hesperiidae, including North American types, were purchased in 1931 by the BMNH from R. Oberthür (Riley 1964).

In the Entomology Library of The Natural History Museum is a loose-leaf typewritten manuscript entitled "List of specimens disposed of by C. Höfer prior to purchase of remainder by the British Museum (Natural History)." It is stamped "C. HOFER, 36, F8 DE PARIS, RENNES (FRANCE)," which was Oberthür's address. The list was conceivably prepared in 1927 by Norman D. Riley, who was then serving as an Assistant Keeper of Entomology in the BMNH. Riley (1927) wrote a detailed account of the purchase of Oberthür's collection and noted that facts about preceding sales of Oberthür's specimens were given to the BMNH; the typewritten list of specimens likely served as a summary of these transactions. Unfortunately, entries on the list have faded and become difficult to read. One section has a handwritten heading of "Dr. Barnes" and inventories the specimens that were sent to W. Barnes in 1925. Apparently based on a similar list from Höfer, the specimens sent to Barnes were labeled upon receipt as "type a/c [according to] Höfer." Although Emmel et al. (1998) believed that Barnes personally penned these labels, they were actually prepared by Foster H. Benjamin, who curated Barnes' collection from 1922-1927. Benjamin signed and dated some of the labels on these specimens (Fig. 14). After Barnes' death in 1930, his collection was purchased the following year by the United States Government for $50,000 and moved to the National Museum in Washington, D.C. (Hewes 1936, Horn et al. 1990).

Boisduval's specimens from California were obtained mostly from a single collector (P. J. M. Lorquin) and their history is reasonably well documented (Emmel et al. 1998), lending credibility to their acceptance as holotypes and syntypes. On the other hand, the "types" that correspond to taxa described in B&L cannot be traced to any particular source. Although Boisduval (1836) claimed that he possessed specimens of almost all the taxa that he described in B&L, he maintained his collection until 1876 and he may have acquired the selected "type" specimens up to 47 years after the original descriptions were published. In addition, not all these "types" are consistent with the written descriptions, suggesting Boisduval based his original characterizations on other specimens or John Abbot drawings. Brown (1965) and Miller & Brown (1981) considered such specimens to be "pseudotypes." Most of the written descriptions in B&L were accompanied by Abbot illustrations and it is safe to assume that the original drawings were at least consulted for all these treatments. The specimens selected as "types" for B&L taxa serve as helpful vouchers and can convey Boisdual's taxonomic concepts, but they cannot automatically be accepted as valid holotypes or syntypes. Some of these "types," especially of Hesperiidae, may correspond to specimens from Boisduval's collection that were drawn by Blanchard for plates in B&L. If so, a careful comparison against the original drawings in South Carolina may establish such specimens as acceptable types.

Drawings by Blanchard and Abbot. Émile Blanchard's artwork is meticulous, arguably surpassing Abbot in detail and accuracy. It seems inconceivable, but he was only about 15 years old when his drawings in South Carolina were completed. Blanchard was extraordinarily gifted and his father was also a natural history illustrator. Like contemporary French entomologist Pierre Hippolyte Lucas, Blanchard began work in the Muséum National d'Histoire Naturelle in Paris at a young age. Lucas was just 13 years old when he was hired to apprentice in the zoology laboratory while Blanchard was 14 when he accepted a temporary position in the entomology laboratory (Gaudry 1900, Lesne 1901). Beginning in his teens, Blanchard published on many subjects, including insects, mammals and fish. He was probably introduced to Boisduval when he started working at the museum (ca. 1833) and this is consistent with Boisduval's use of Blanchard drawings for plates in various publications at that time, including Boisduval (1833, 1836) and Boisduval et al. (1832-1837). Duménil and Borromée were also the master engravers for these works, and Duménil served as the publisher for Blanchard (1840). The first plate issued in B&L from an illustration by Blanchard was Plate 35, copied from drawing no. 14 in South Carolina and published no earlier than 1833 (dos Passos 1962, Cowan 1969). Blanchard became one of the most celebrated French natural history illustrators of his era, but sadly his eyesight deteriorated over the course of his lifetime, resulting in total blindness in his later years (Gaudry 1900).

In contrast, Abbot was over 60 years old when Le Conte commissioned him for the drawings in South Carolina. Out of convenience, Abbot often relied on template drawings that he developed earlier in his career to produce duplicate renderings of insects, as well as birds (Simpson 1993, Gilbert 1998). Consequently, Abbot's drawings in South Carolina share numerous figures with his other original and published illustrations. I compared Abbot's 105 Lepidoptera drawings in South Carolina with his 95 Lepidoptera illustrations completed between 1816 and 1818 for English Naturalist William Swainson that are now deposited in the Alexander Turnbull Library, Wellington, New Zealand. Fully 142 figures of adults and early stages are duplicates. At least ten of the butterfly species treated in both B&L and Smith & Abbot (1797) share identical figures of early stages. Baker (1959) noted that plates in B&L resembled some of the original Abbot drawings in Emory University. In his exhaustive treatment of geometrid moths, Packard (1876) copied twenty-three figures of adults and early stages from "Abbot MS [manuscripts]." Many of these figures are identical to those on drawings in South Carolina, but Packard doubtless copied them from other Abbot watercolors once owned by A. G. Oemler and Cambridge botanist Asa Gray. At that time, these drawings were deposited in the library of the Boston Society of Natural History where Packard served as acting librarian and custodian in 1865 (Mallis 1971). They were procured in 1946 by Harvard University.

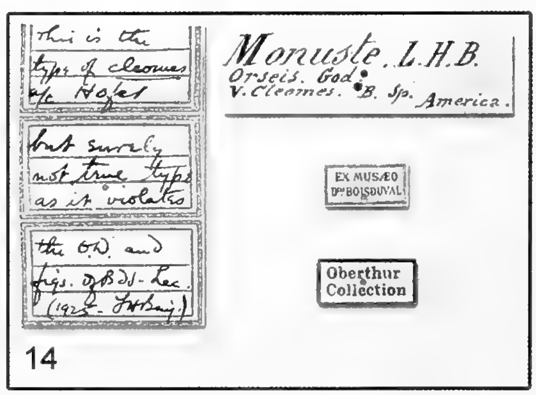
Hillhouse (1985) aptly described Abbot's artwork as "true in color, subtle and full of light, exact in size, and with detailed accuracy." Nonetheless, a few of Abbot's illustrations in South Carolina lack much of the painstaking detail of his earlier watercolors. The engravers and colorists were often criticized for the imprecision of many plates in B&L, which may have resulted in Duménil's early departure from the project (Cowan 1969). It can now be seen that Abbot himself was also responsible for some of the inaccuracies.

Besides *M. ismeria* (Plate 46), another problematic illustration in B&L was that of *Thecla liparops* Le Conte (=*Satyrium liparops*) (Plate 31, figs. 1-2). Edwards (1872) thought the published figures of *T. liparops* were "a wretched attempt" at copying the work of Abbot, adding, "the species has puzzled lepidopterists, nothing like that plate having been seen in nature." Michener & dos Passos (1942) similarly remarked that the ventral figure on the published plate "does not agree with any butterfly known to the authors." Forbes (1943) assumed that details of Abbot's original drawing had been "tampered with" on the plate. Gatrelle (2001) also thought the published figures of *T. liparops* were surely inferior to Abbot's original drawing. Drawing 12 in South Carolina demonstrates that Abbot's figures were poorly executed and the published plate was a faithful reproduction (Figs. 3, 6, 7). Although the colorists were sometimes a bit too liberal with their use of blue on the plate, the overall design is the same. Abbot's drawing for *T. liparops* confounded even Boisduval, who argued that it had "la plus grande resemblance avec la Favonius de Smith" [the most greatest resemblance with the Favonius of Smith]. Boisduval so disagreed with Le Conte over the identity of the depicted species that he ceded authorship of the name to Le Conte. The identity of this taxon remained in some doubt for over a century.

Original moth drawings. Moth drawings in South Carolina were almost certainly destined for use in preparing the plates for another installment of *Histoire Générale*. Boisduval planned to continue the project with a volume on moths, but it was never realized

(Cowan 1969). French entomologist Achille Guenée consulted a set of Abbot drawings for descriptions and plates in his multivolume treatise on moths (Guenée 1852-1858), but the whereabouts of these drawings was unknown (Gall & Hawks 2002). In the preface to his first volume on noctuid moths, Guenée referred to a set of Abbot drawings provided to him by Boisduval. Guenée described them as being accompanied by the figures of the caterpillar and he erroneously related that the renderings were intended for the continuation of Smith & Abbot (1797). Oberthür (1920), who was personally acquainted with both entomologists, revealed that Boisduval had loaned Guenée the Abbot drawings now in South Carolina (and probably also the missing hostplant drawings). Upon a recent examination of these drawings, Lawrence F. Gall confirmed that they were likely among those consulted by Guenée. A more thorough examination of Guenée (1852-1858) is required to determine if any published figures were copied from these Abbot drawings. Émile Blanchard also provided some of the original drawings for Guenée's published plates. Sixteen smaller moth drawings in South Carolina (nos. 58, 66, 67, 70, 82, 84, 85, 87, 88, 90, 92, 103, 104, 107, 114, 115) are crude relative to Abbot's work and were rendered on darker paper. J. E. Le Conte, a less talented illustrator, may have been the artist as suggested by a reference to "Leconte" on drawing 90.

The true identity of *Pieris cleomes*. This taxon was described in B&L on pages 43-45 and figured on Plate 16 from a drawing by John Abbot. The written description characterized the male and included brief remarks about the female and early stages. The plate included dorsal and ventral males, dorsal female, larva on a host leaf, and pupa (Fig. 8). The text stated, "il habite la Géorgie et la Virginie, mais il y est assez rare; il est plus commun dans la Floride" [it lives in Georgia and Virginia, but it is rather rare there; it is more common in Florida]. The dorsal adults in the plate have more distinct black wing borders than generally found in the Florida subspecies *Ascia monuste phileta* (Fabricius). Subsequent interpretations of *cleomes* varied. The first was Boisduval himself who wasted no time in treating *cleomes* as a variety of *Ascia monuste* (L.) (Boisduval 1836). Despite Boisduval's revised treatment, Doubleday (1844) listed three specimens from Honduras in the British Museum as *P. cleomes*. Röber (1909) called *cleomes* a form of *A. monuste* from "the south of North America" and characterized it as "somewhat smaller and less blackly marked." Talbot (1932) listed it as a subspecies of *A. monuste* from the southern United States. Comstock (1943) proposed that *cleomes* "might be properly applied to a subspecies with a more northern range than *phileta*." Chermock (1946) also treated *cleomes* as a subspecies of *A. monuste* and suggested that it must have been a small population that eventually became extinct. Klots (1951) observed that *cleomes* "resembled *m. monuste* rather than *phileta*," and likewise believed it was "possibly a now extinct or diluted subspecies of the coastal plain from Georgia onwards." dos Passos (1964) synonymized *cleomes* under nominate *A. monuste*. Harris (1972) distinguished *cleomes* as having a "slightly wider and continuous black border on the forewings" and thought that Abbot may have figured a heavily marked individual of *A. m. phileta*. Howe (1975) referred to "unresolved problems related to *cleomes*" and treated it as a possibly extinct subspecies that did not possess a dark form of the female as in *A. m. phileta*. Miller & Brown (1981) and Ferris (1989) listed *cleomes* as a subspecies of *A. monuste*, but Ferris thought it might apply to a "pale migratory form of *A. m. phileta*." Most recently, Gatrelle (2000) also considered this butterfly to



FIGS. 13-14. Unacceptable "type" specimen of *Pieris cleomes*. **13,** Dorsal (left) and ventral of male *A. m. orseis* from Boisduval's collection. **14,** Specimen labels.

represent the "never before collected" subspecies *A. m. cleomes*.

Abbot's drawing 7 of *A. monuste* in South Carolina includes a penciled reference to Plate 16 of B&L (Fig. 10). Boisduval wrote the name "*Pieris orseis* God." on the drawing, obviously in his attempt to compare the figures with what is now recognized as *Ascia monuste orseis* (Godart). He also discussed orseis in the texts of B&L and Boisduval (1836). Sets of Abbot drawings in The Alexander Turnbull Library (Wellington, New Zealand), The Houghton Library (Harvard University), and The Natural History Museum, London, contain exact duplicates of a larger rendering of *A. monuste* that portrays the same adults and early stages as those in drawing 7 in South Carolina and B&L Plate 16 (Figs. 8-10). However, the larger drawings also portray a dark female (Fig. 9). This dark form is characteristic of *A. m. phileta* and contradicts the notion of Howe (1975) that *cleomes* lacks dark females. The published plate also included a plant leaf that matches a portion of the hostplant in the larger drawings (Figs. 8, 9). A comparison of Abbot's notes demonstrates that Boisduval possessed yet another duplicate of Abbot's larger rendering of *A. monuste* (Table 2). Abbot's notes for each drawing are as follows:

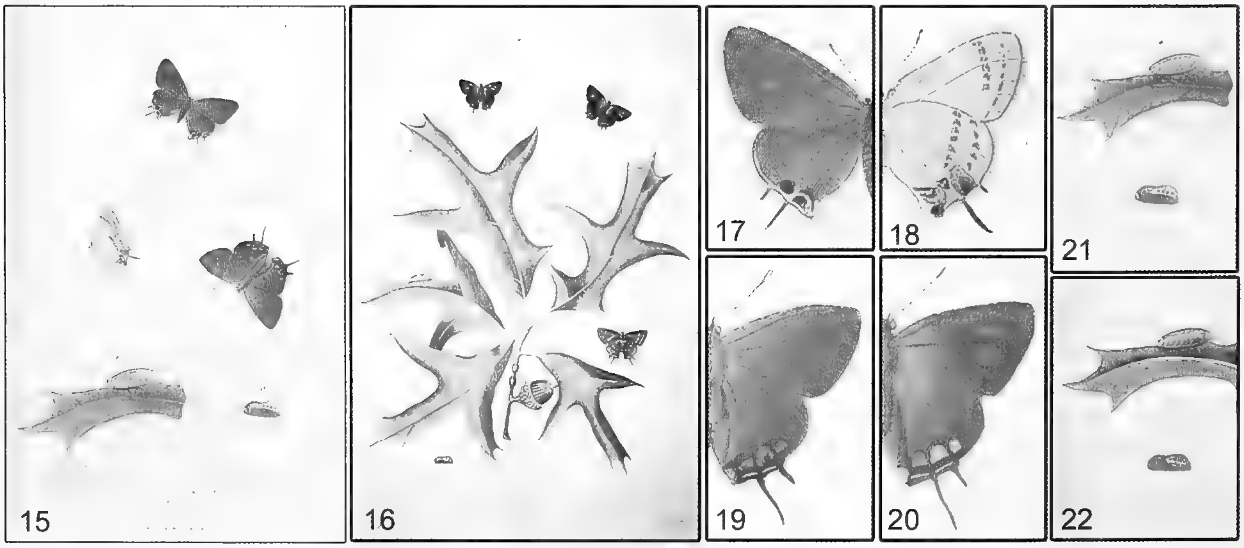
1. For John Francillon, ca. 1805-1810 (The Natural History Museum, London; see Gilbert 1998, Pl. 29): "The White Butterfly. Papilio Danaii candidi. The caterpillar feeds on the plant figured. It tyed itself up 16th July and changed in the chrysalis 17th and bred 23rd. near half the female Butterflies varies being a dingy black as figured. They continue in plenty about Savannah all this last summer but I have rarely seen any for the last twelve years. I am indebted for this discovery of the caterpillars to my friend Mr. Oemler who first found it in his garden in Savannah." [although this volume of drawings is dated 1804, Abbot did not meet Oemler until 1805].
2. For Augustus G. Oemler, ca. 1810 (Houghton Library, Harvard University; see Rogers-Price 1983, catalog fig. 10): "Pap. Danai Cleome. Feeds on the Cleome Pentaphilles. Tyed up16th July. Changed 17th bred 23rd nearly half of the female Butterflies varies being a dingy black as figured, Some years they are in plenty about Savannah, but in others very rare if to be met with at all. I am indebted for the discovery of this Caterpillar to my friend Mr. Oemler who first met with it in his garden in Savannah."
3. For J. E. Le Conte, ca. 1815-1820 (given to Boisduval) (Houghton Library, Harvard University; notes only): "White Butterfly. Danai Cleome. Feeds on the Cleome pentaphilles. Changed 17th July, bred 23rd July. nearly half of the female Butterflies varies being of a Dingy colour, as figured, They are generally rare, but some years at intervals are very plenty in the lower parts of the Country, I am indebted for the discovery of the caterpillar of the Species to my friend Mr. Oemler, who first found it in his garden in Savannah."
4. For William Swainson, ca. 1817 (Alexander Turnbull Library, Wellington, New Zealand; Fig. 9): "Papilio Danai Cleome. Feeds on the Cleome Pentaphilles. Tyed up 16th July, changed 17th, bred 23rd. many of the female Butterflies varies being of a dingy black as figured. This Butterfly is some Summers very plenty in Savannah but is rare in the Inland parts."

The Latin names that Abbot used for this species were based on the Linnaean classification system, where Papilio was the genus, Danai (or Danaii) was a group that included the Pieridae, Candidi was a subdivision of white butterflies, and Cleome was the name coined by Abbot based on the hostplant. The text for *P. cleomes* in B&L stated, "Cette chenille vit dans les jardins, sur le cleome pentaphylla" [this caterpillar lives in the gardens, on the *cleome pentaphylla*] and was obviously excerpted from Abbot's notes for the hostplant drawing that Boisduval possessed (3 above; Table 2). Abbot correctly identified the hostplant in his drawings as *Cleome gynandra* L. (= *C. pentaphylla*) (Capparaceae). Le Conte wrote "Cleome" on drawing 7 in South Carolina, undoubtedly in reference to the name or hostplant given in Abbot's notes. The adult figures of *P. cleomes* in B&L were evidently copied from drawing 7 (Fig. 10), while the host leaf was taken from the missing hostplant drawing that was analogous to surviving copies (Fig. 9).

Abbot's observations mirror the modern occurrence of *A. m. phileta* in coastal Georgia, which Harris (1972) defined as "fairly common at times, especially near or on the coastal islands, it is very sporadic in occurrence. Further inland it becomes infrequent to very rare." The text of B&L even referred to the more common occurrence of the butterfly in Florida where *A. m. phileta* is most abundant. This subspecies is migratory and adults sometimes reach more northern coastal areas in great numbers, such as in June 1881 when thousands were recorded in Bluffton, South Carolina (Williams 1930). Bluffton, Beaufort County, South Carolina is located 40 km (25 mi) north of Savannah, Georgia where Abbot observed *A. monuste*. Adults of *A. m. phileta* are extremely variable and individuals from peninsular Florida routinely present the same dorsal and ventral characteristics as the figures in Abbot's drawings. Abbot's illustrations and observations, as well as the comments in B&L, are referable to *A. m. phileta*. *Pieris cleomes* is therefore synonymous with *A. m. phileta* and the engraver, P. Duménil, simply exaggerated some of the pattern elements (Figs. 11, 12). This finding is more plausible than the fanciful theory that *P. cleomes* represented an extinct subspecies. Miller & Brown (1981) gave the type locality of *P. cleomes* as "probably Screven Co., Georgia." In view of Abbot's notes, I hereby amend the type locality to Savannah, Chatham County, Georgia. As the identity of the intended butterfly is now apparent, and *P. cleomes* is not involved in any complex zoological problem, there is no exceptional need to designate a neotype to objectively define the taxon.

Finally, it must be mentioned that there is a male *A. monuste* from Boisduval's collection in the NMNH that was sent to W. Barnes as the type of *P. cleomes* (Fig. 13). It was listed as "*Pieris monuste cleomes* Bdv. & Lec." on the typewritten list of specimens that were purchased from the Oberthür collection by W. Barnes (list in The Natural History Museum, London). The original determination label, not written by Boisduval (Depuiset?), reads "*Monuste* L. H. B./*Orseis*. God./v. *Cleomes*. B. Sp./ America" (Fig. 14). The three letters "L. H. B." probably refer to the name *monuste* as published by Linnaeus, Hübner, and Boisduval. "*Orseis*" and "*Cleomes*" were written in smaller handwriting directly below "*Monuste*," obviously as synonyms following the treatment in Boisduval (1836). The line "v. *Cleomes*. B. Sp." likely means "variété Cleomes [as treated by] Boisduval [in] Species Générale." Also present are three conjoined red-bordered labels, written by F. H. Benjamin, that read, "This is the type of *cleomes* a/c Hofer, but surely not true type as it violates the O.D. and figs. of Bdl.-Lec. (1925-J. H. Benj.)" (Fig. 14). As indicated by Benjamin, this specimen is contrary to the original description of *P. cleomes*. In the text of B&L, Boisduval compared *P. cleomes* to *monuste* and *orseis*, noting that the ventral hindwings of *cleomes* are less brown, the dorsal forewings lack elliptical white spots at the apex, and the dorsal hindwings of the male lack a series of black marginal spots. The "type" specimen in the NMNH (Fig. 13) boldly exhibits all these features and is consistent with the South American subspecies *A. m. orseis*. Again, this demonstrates that such Boisduval "type" specimens for B&L taxa were arbitrarily selected on the basis of existing determination labels that included applicable names.

The true identity of *Thecla favonius* in Boisduval & Le Conte (1829-[1837]). Plate 30 in B&L was identified as *Thecla favonius* from the "les parties méridionales des Etats-Unis" [the southern parts of the United States]. P. Duménil was credited as the artist, but in the text Boisduval attributed the figures to Abbot. The plate depicted dorsal and ventral males, dorsal female, larva on a host leaf, and pupa (Fig. 15). In an "Observation" following the treatment of *T. favonius* in B&L, Boisduval wrote that he doubted his *favonius* was the same species described and illustrated as *Papilio favonius* in Smith & Abbot (1797) (= *Satyrium favonius*) (Fig. 16). He suspected that his *favonius* was synonymous with *Papilio melinus* Hübner (= *Strymon melinus*), whereas the butterfly described in B&L as *Thecla liparops* was akin to the *favonius* of Smith & Abbot (1797). To further complicate matters, Boisduval also figured *S.*



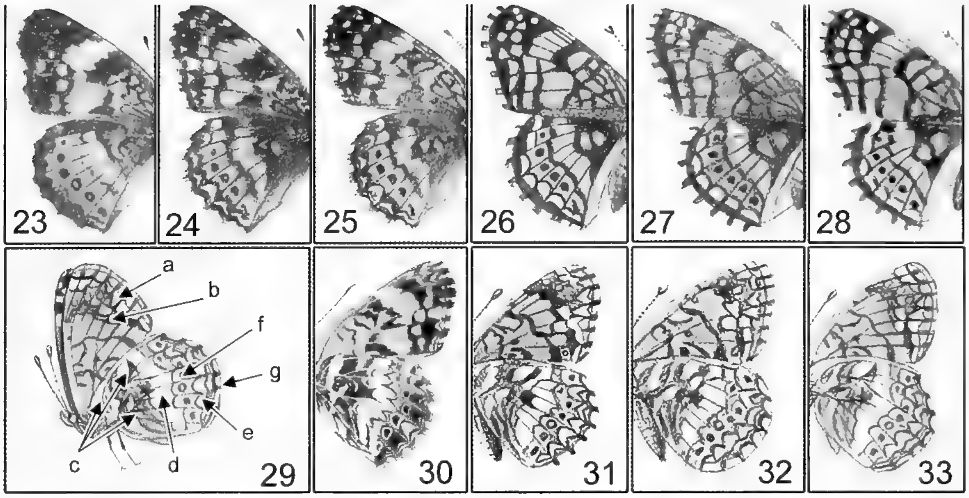
FIGS. 15-22. *Thecla favonius*, Plate 30 in Boisduval &Le Conte (1829-[1837]) (B&L) and *Papilio favonius*, Plate 14 in Smith & Abbot (1797) (S&A). **15,** *T. favonius*, B&L. **16,** *P. favonius*, S&A. **17,** Dorsal male *S. melinus*, B&L. **18,** Ventral male *S. melinus*, B&L. **19,** Dorsal female, B&L. **20,** Dorsal female, S&A. **21,** Larva and pupa, B&L. **22,** Larva and pupa, S&A.

melinus on Plate 28 and described it as *Thecla hyperici* Boisduval & Le Conte. The association of these various figures and names created nomenclatural chaos that persisted for decades. Morris (1862) complained, "There is an almost inextricable confusion in the determination of these species." Sixty years later, Oberthür (1920) bemoaned that Boisduval's treatment resulted in "un manque fâcheux de clarté" [an annoying lack of clarity]. Harris (1841) was the first to associate the *favonius* of B&L with *S. melinus* when he noted that it was the same as the species he described as *Thecla humuli*, now considered a subspecies of *S. melinus*. In his copy of B&L, Cyril F. dos Passos wrote on Plate 30, "= *melinus* Hbn." However, this synonymy is only partially correct.

Oberthür (1920) accurately determined that the dorsal male in B&L Plate 30 was *S. melinus* (Figs. 17, 18), but observed that the female was a different, unidentified species. A comparison of this female figure with other illustrations by Abbot reveals that it is equivalent to the female of *S. favonius* on Plate 14 of Smith & Abbot (1797), but was inexplicably colored to portray a darker butterfly (Figs. 19, 20). The larva, pupa, and host leaf also correspond to the plate of *S. favonius* in Smith & Abbot (1797) (Figs. 21, 22). Therefore, the *favonius* of B&L is synonymous with both *S. melinus* and *S. favonius*. Abbot (in Smith & Abbot 1797) called the figured hostplant "fork leaved black jack." Although J. E. Smith (in Smith & Abbot 1797) identified it as *Quercus rubra* L. (Fagaceae), it most closely resembles *Quercus laevis* Walter (Fagaceae), for which "black jack" is a colloquial name in the region where Abbot resided (M. A. Garland, R. P. Wunderlin pers. com.). Nineteenth century Florida botanist Alvan W. Chapman suspected that Abbot's references to "black jack" represented *Quercus catesbaei* Michx. (Fagaceae) (Scudder 1888-1889), now considered a synonym of *Q. laevis*. Abbot's original drawings for Smith & Abbot (1797) are currently deposited in the John Work Garrett Library of the Johns Hopkins University. The Linnean Society of London preserves his accompanying notes.

The story of B&L Plate 30 does not end there. Boisduval remarked in B&L that the larva in the Abbot drawing used for Plate 30 was the same as the one figured in Smith & Abbot (1797), but the adults were consistent with *T. hyperici* (= *S. melinus*). This infers that Abbot mistakenly inserted adult figures of *S. melinus* into one of his hostplant drawing of *S. favonius*. This assertion seems unlikely, especially if we are also to believe that Abbot altered the coloration of his female *S. favonius* to more closely resemble *S. melinus*. Furthermore, the figures of *S. melinus* in Plate 30 are dissimilar to Abbot's other representations of this species. There are also no entries in Abbot's notes at Harvard that correspond to a third drawing of *S. melinus*. As credited on Plate 30, Duménil was probably responsible for these figures and he based them on a specimen in Boisduval's collection. Abbot's notes at Harvard also lack an appropriate entry for a drawing of *S. favonius*, suggesting Duménil copied the female and early stages from Plate 14 of Smith & Abbot (1797). Perhaps Boisduval desired to reconcile *favonius* and instructed Duménil to include both interpretations of this taxon. Plate 30 is unquestionably the most peculiar plate in B&L.

The true identity of *Melitaea ismeria*. According to Cowan (1969), the most accurate publication date for *M. ismeria* in B&L is 1835, not 1833 as reiterated by other authors. This includes Calhoun (2003), in which I provided evidence that *M. ismeria* is synonymous with C. gorgone, rather than *C. nycteis* as proposed by Gatrelle (1998). The original description of *M. ismeria* in B&L is an accurate portrayal of the figures in Abbot's drawing 24 in South Carolina. Based on a faulty translation of the description of the ventral wings, Gatrelle (2003) argued that the written account was likely derived from a specimen of *C. nycteis*. Following is the description of the ventral wings as it appeared on pages 168-169 of B&L with a translation that corresponds to Abbot's original drawing (Fig. 29) (see Calhoun (2003) for a color reproduction): "Le dessous des supérieures differe du dessus en ce que, avant le bord postérieur, il y une bande blanche maculaire, précédée de trois ou quatre taches de sa couleur. Le dessous des ailes inférieures est fauve, avec des taches blanches vers la base, puis une bande médiane irréguliere, transverse, et enfin des lunules marginales de la méme couleur; celles-ci sont separées de la bande transverse par une série de points noirâtres correspondant à ceux du dessus. La frange de toutes les ailes est noiratre entrecoupée de blanc" [The underside of the forewing differs from the upperside in that, before the posterior edge, is a white macular band (a), preceded by three or four spots of its color (b). The underside of the hindwing is fawn, with white spots towards the base (c), then an irregular median band, transverse (d), and lastly marginal lunules of the same color (e); these are separated from the transverse band (d) by a series of blackish points (f) corresponding to those of the upperside. The fringe of all the wings is blackish intersected by white (g)]. Gatrelle (2003) misapplied the fawn ("tawny") color to the median band and lunules of the hindwing. In so doing, he confused these characters with other pattern



FIGS. 23-33. *Chlosyne* specimens and Abbot figures. **23,** Dorsal *C. nycteis* female, 16.vi.1996, Jackson Co., Florida (leg. J. V. Calhoun) [=*C. ismeria ismeria* of Gatrelle (1998)]. **24,** Dorsal *C. gorgone* female, 28.iv.2003, Hancock, Burke Co., Georgia (leg. J. V. Calhoun) [=*C. g. gorgone* of Gatrelle (1998)]. **25,** Dorsal *C. g. carlota*, 7.v.1972, Jasper Co., Georgia (FSCA). **26,** Abbot's dorsal female,° London. **27,** Abbot's dorsal female, New Zealand (ref. no. E-272-f-017). **28,** Abbot's dorsal female, South Carolina°°. **29,** Abbot's original ventral figure for *M. ismeria* (characters correspond to text). **30,** Ventral *C. gorgone*, 28.iv.1995, Orangeburg Co., South Carolina (ex. ovum, FSCA) [=*C. g. gorgone* of Gatrelle (1998)]. **31,** Abbot's ventral figure°, London. **32,** Abbot's ventral figure, New Zealand. **33,** Abbot's ventral figure, South Carolina°°. (°© The Natural History Museum, London; °°Thomas Cooper Library, University of South Carolina)

elements. Furthermore, the original description clearly defined the lunules as being separated from the median band by blackish points, not "punctuated" by points as indicated by Gatrelle's translation.

Drawing 24 in South Carolina is one of at least four drawings by John Abbot that depict analogous figures of *C. gorgone*, though his attention to detail varied. Abbot referred to Burke County, Georgia in his notes for three of these drawings. Gatrelle (1998) characterized populations of *C. gorgone* currently found in extreme eastern Burke County and adjacent portions of South Carolina as a univoltine (April-early May) subspecies, *C. g. gorgone*. The dorsal surface of a female *C. gorgone* that I collected in April 2003 in eastern Burke County is reminiscent of Abbot's female figures (Figs. 24, 26-28), which are unlike *C. nycteis* from the region (Fig. 23). The ventral surfaces of some individuals of the single-brooded phenotype of *C. gorgone* are also consistent with Abbot's ventral figures (Figs. 30-33). However, Abbot's drawings more closely resemble specimens tentatively recognized as the widespread subspecies *C. g. carlota* (Reakirt) (Fig. 25). The ventral surface of a pre-1840 Georgia specimen of *C. gorgone* in The Natural History Museum, probably collected by Abbot and identified by Gatrelle (2003) as *C. g. carlota*, is extremely similar to Abbot's ventral illustrations (Calhoun 2003, figs. 23, 24). Populations attributed to *C. g. carlota* tend to be slightly paler and are multivoltine in Georgia, with adults flying from April to September (Harris 1972). A record from Houston County, located within the same physiographic section of Georgia as Burke County, is dated 3 June (Harris 1972). This is compatible with the adult emergence date of 26 May given in Abbot's notes (though Abbot's rearing conditions could have altered development). This can also account for the blooming *Helianthus divaricatus* (L.) (Asteraceae) hostplant in three of Abbot's duplicate drawings; this plant flowers after the flight period of the single-brooded populations of *C. gorgone*. It is notable that the dorsal painting of a male *C. g. carlota* by Howe (1975, Pl. 40, fig. 1) is remarkably consistent with the male figure by Abbot (Calhoun 2003, figs. 3, 22). The proximity of occurrence and relationship of the perceived *C. gorgone* phenotypes in Georgia are unknown. Abbot traveled over large portions of southeastern Georgia in search of specimens and his reference to Burke County does not exclude the possibility that he encountered *C. gorgone* in other areas. Gatrelle (2003) believed that the adult butterflies in Abbot's drawings are unlike any taxon in the eastern United States and proposed that they represent "composites" of *C. gorgone* and *C. nycteis*. I see no evidence of this.

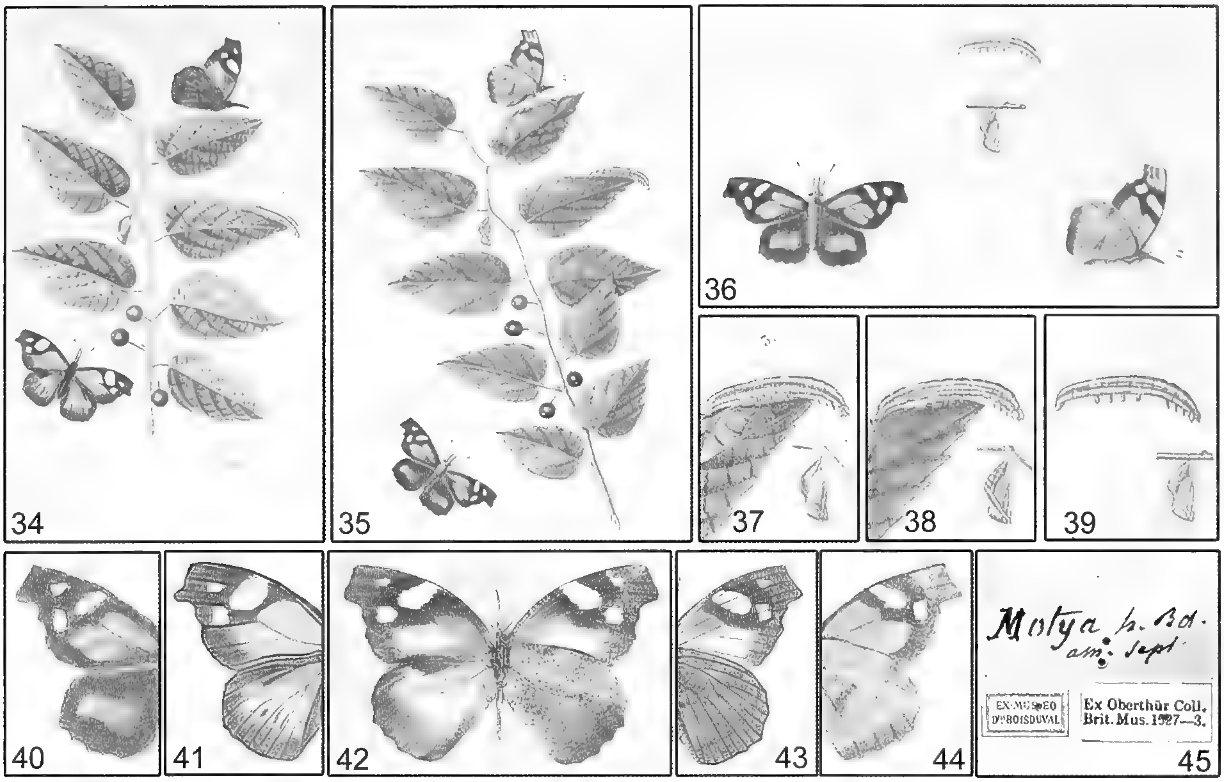
The right half of Abbot's dorsal figure of *C. gorgone* in South Carolina is more refined, thus it was used to create the dorsal engraving of *M. ismeria* in B&L (Calhoun 2003, figs. 8,9). However, the left half (Fig. 28) is more faithful to Abbot's other versions of the same figure. A close examination of the adult figures in this drawing revealed no subsequent alterations to wing shape or design. Abbot simply rendered these figures with less devotion to his template, contributing to 170 years of confusion.

Doubleday (1847) named *Melitaea nycteis* in connection with an accurate engraving of the female holotype (in The Natural History Museum, London), but failed to provide a written description. He did not consider *M. nycteis* to be the same as *M. ismeria*, which he associated with the species now recognized as *C. gorgone* (Calhoun 2003). Boisduval's own concept of *C. nycteis* apparently also differed from that of *M. ismeria*. Boisduval (1869) listed *Melitaea nycteis* and characterized it as approaching the appearance of *M. ismeria*, but he did not suggest they were conspecific. Boisduval published this treatment 34 years after he described M. ismeria, and 22 years after Doubleday had named *M. nycteis*. Although Boisduval (1869) referred to *nycteis* from California where it is not known to occur, he was likely familiar with this widespread North American species by that time. There was little potential for misidentification, as Boisduval (1852, 1869) considered the most similar California species to represent different taxa (see Emmel et al. 1998). Boisduval was presumably confused about the source of some of his specimens, as he also listed several other species not validly recorded from California (J. F. Emmel pers. com.). The specimens listed by Boisduval as *C. nycteis* have not yet been located. If correctly identified, they were likely from the eastern United States where the majority of Boisduval's American specimens originated. During the preparation of Doubleday et al. (1846-1852), in which *M. nycteis* was first named and figured, Boisduval provided the authors access to his personal collection and even loaned them specimens for reproduction on their color plates (Oberthür 1880). Like many entomologists of his day, Doubleday took specimens to Boisduval for evaluation. Doubleday mentioned one such trip in 1841 when he wrote, "should I go merely for a short visit to France I mean to take a host of things for Boisduval's inspection" (Scudder 1869). Doubleday freely loaned and gave away specimens to other researchers, sometimes to the detriment of the collections in his care (Salmon 2000). There was ample opportunity for Doubleday to discuss the identity of *M. ismeria* and *M. nycteis* and compare specimens with Boisduval.

Additional new evidence indicates that Boisduval ultimately possessed at least one specimen that he identified as *ismeria*. The typewritten list in The Natural History Museum, itemizing the Boisduval "types" that were sent to W. Barnes in 1925, has a ticked entry for "*Phyciodes ismeria*." The use of the genus *Phyciodes* reflects prevailing usage at the time the list was created (ca. 1927), as Boisduval's determination labels typically included only the species name. The specimen has not been found in the NMNH and its fate remains a mystery, yet there are two valuable clues to its identity. J. H. McDunnough, who ostensibly selected this specimen in 1913 to serve as the type of *M. ismeria*, and F. H. Benjamin, who would have accessioned this "type" into the Barnes collection in 1925, both subsequently coauthored checklists of Lepidoptera with Barnes in which they considered *ismeria* to be synonymous with *gorgone* (Barnes & McDunnough 1917, Barnes & Benjamin 1926). Prior to moving the massive Barnes collection from Decatur, Illinois to Washington, D. C., workers spent two weeks "ramming home" the 300,000 insect pins to prevent the attached specimens from jarring loose in transit (Hewes 1936). The missing "type" of *M. ismeria* was perhaps a casualty of this process.

The true identity of *Libythea motya* in Boisduval & Le Conte (1829-[1837]). Abbot is also credited with rendering the original drawing for Plate 64 in B&L of *Libythea motya* (Fig. 34). Many authors, such as Morris (1862), Seitz (1916), Riley (1975), Miller & Brown (1981), and Smith et al. (1994) incorrectly attributed the original description of *motya* to this plate in B&L, but Hübner (1819-[1827]) was actually the first to figure this Cuban species, as *Hecaërge motya* (Plate [137], figs. 1-2). No textual reference accompanied the plate of *Libythea motya* in B&L. Because of the perceived connection of the original drawing to Abbot, the figured specimens were thought to have come from Georgia. Harris (1972) speculated that Abbot may have captured a rare Cuban stray or acquired it from a source outside Georgia. Miller & Brown (1981) observed that the illustration seems to depict the Cuban butterfly, but suspected it actually represented a "genetic throwback" of the eastern North American subspecies, *Libytheana carinenta bachmanii* (Kirtland).

The plate of *Libythea motya* in B&L was obviously based on an Abbot hostplant drawing of *L. c. bachmanii* that was a duplicate of another Abbot illustration now in New Zealand (Fig. 35). Abbot's manuscript notes for the drawing in New Zealand are identical to his notes at Harvard University that likely accompanied the drawing used for the published plate (Table 2). Boisduval gave Scudder the notes now at Harvard and Scudder's handwritten name "*bachmanii*" is found next to Abbot's entry for this species. For his treatment of *bachmanii*, Scudder (1888-1889) obtained the information "Georgia 'rare' (Abbot)"



FIGS. 34-45. *Libytheana c. bachmanii* and *L. motya*. **34,** B&L Plate 64 identified as *Libythea motya*. **35,** John Abbot's drawing of *L. c. bachmanii*, New Zealand (ref. no. E-272-f-018). **36,** Drawing 38° of *L. c. bachmanii*. **37,** Larva and pupa, B&L Plate 64. **38,** Larva and pupa from Abbot's drawing, New Zealand. **39,** Larva and pupa from Abbot's drawing 38°. **40,** Dorsal figure of *L. c. bachmanii*, New Zealand. **41,** Dorsal figure of *L. motya*, B&L Plate 64. **42,** Dorsal (left) and ventral of male *L. motya* specimen from Boisduval's collection. **43,** Ventral figure of *L. motya*, B&L Plate 64 (image reversed). **44,** Ventral figure of *L. c. bachmanii*, New Zealand (image reversed). **45,** Three labels from Boisduval's specimen of *L. motya*. (° Thomas Cooper Library, University of South Carolina)

from these notes. Drawing 38 in South Carolina also portrays identical figures of *L. c. bachmanii*, but without the sprig of the hostplant, *Celtis tenuifolia* Nutt. (Celtidaceae) (Fig. 36). The early stages and hostplant on B&L Plate 64 are identical to Abbot's drawings of *L. c. bachmanii* (Figs. 37-39), but the adult figures are quite different (Figs. 40, 41, 43, 44). The wings are broader and the palpi are more elongated. The forewing apical spots are inconsistent with his other drawings and the hindwings are rounded, not squared and deeply scalloped as in *L. c. bachmanii*. The dark brown coloring on the dorsal hindwings is much less extensive and the ground color of the ventral hindwings is dark, speckled with black spots. These deviations from Abbot's figures are too great to simply dismiss as a poor engraving.

An overlooked discovery by S. H. Scudder provides extraordinary insight into this mystery. Scudder (1888-1889) wrote, "I have examined in Boisduval's collection the butterfly figured in Boisduval and Le Conte's work on North American butterflies, under the name of *Libythea motya*, and it is the West Indian species, *Hypataus terena* (Godart) the occurrence of which in the United States is unknown; the caterpillar and chrysalis, however, are from Abbot's drawings, and represent our common species [*L. c. bachmanii*]." Scudder most likely saw this specimen during his trip to Paris when he also examined the Abbot drawings now in South Carolina and obtained Abbot's notes at Harvard. Although he identified the specimen as the Hispaniolan species *Libytheana terena*, Scudder (1875) also called the published figures "a Cuban species," thus he considered *L. motya* to be synonymous with *L. terena*. Contemporaries of Scudder, such as Gundlach (1881), also placed *L. motya* within the synonymy of *L. terena*. The relationship of these taxa is still uncertain, but minor genitalic differences and a lack of intermediates suggest they are separate species (Kawahara 2001, Kawahara pers com.). Scudder must have used drawing 38 in South Carolina (Fig. 36) to confirm that the larva and pupa in B&L Plate 64 (Fig. 34) were from Abbot. Drawing 38 is listed in Scudder's personal notes (Harvard University) and he also published a copy of the figured pupa (Scudder 1888-1889) (Table 1). Probably following Scudder's observations, Kirby (1896) also noted that only the early stages of B&L Plate 64 (figs. 3, 4) represented *L. c. bachmanii*.

To confirm Scudder's claim, the National Museum of Natural History (USNM, Washington, D C.) and The Natural History Museum, London, were searched for specimens of *L. motya* and *L. terena* from Boisduval's collection. Nothing was found in the NMNH, but a single male *L. motya* was discovered in drawer no. 5445 of the Oberthür collection in London (Fig. 42). It has two printed labels that read, "EX-MUSAEO/Dris. BOISDUVAL" and "Ex Oberthür coll./Brit. Mus. 1927—3." It also has two handwritten labels that read, "Motya h. Bd./am. Sept." and "Hecaërge Motya,/Hübn. (Samml. exot./schmett. II Vol. pl.34./fig.3,4) = ne ressemble pas / beaucoup a la fig. de Hübn./est intermediaire entre la / fig. 1 & la fig. 3" [(Sammlung exotischer schmetterling Vol. II, Plate 34, figs. 3, 4) = does not much resemble the figure of Hübner, is intermediate between the fig. 1 and the fig. 3]. The determination label (Fig. 45) was written by Boisduval and is consistent with his other known labels (Horn et al. 1990). The abbreviations 'h." and "Bd." probably refer to the name *motya* as published by Hübner and Boisduval. Again, his abbreviation "am. Sept," refers to Amérique Septentrionale (northern [North] America). The other handwritten label is from C. M. Oberthür (Horn et al. 1990) and refers to the figures of Hübner (1819-[1827]), who illustrated two species under the name of *Hecaërge motya*: *L. motya* (figs 1-2, as the male) and *L. terena* (figs. 3-4, as the female). This is probably the same specimen that Scudder identified as the model for B&L Plate 64 (Figs. 41-43). Boisduval evidently ordered the reproduction of all the elements of Abbot's hostplant drawing of *L. c. bachmanii*, but substituted the adults with figures taken from his own specimen. *Libythea motya* of B&L is therefore synonymous with both *Libytheana motya* (adults) and *L. c. bachmanii* (early stages). Scudder (1888-1889) noted that, "*bachmanii* was also in Boisduval's collection, separated from the other [*motya*], but without name." *Libythea bachmanii* was not described until 1851 and previous authors considered all American specimens to represent *L. motya* (following B&L, not Hübner). Boisduval obviously chose to illustrate the butterfly that most closely resembled the male figures in Hübner (1819-[1827]). There is no surviving original drawing of Boisduval's *L. motya*, suggesting Borromée engraved the figures directly from this specimen. This additional evidence disassociates John Abbot from these figures of *Libythea motya* and offers yet another glimpse into the complicated production of the legendary iconography by Boisduval and Le Conte.

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A CRITICAL RESPONSE TO THE PAPER "TOUGH AFRICAN MODELS AND WEAK MIMICS: NEW HORIZONS IN THE EVOLUTION OF BAD TASTE" BY P. DEVRIES PUBLISHED IN THIS JOURNAL, VOL. 57(3), 2003

P. DeVries has published two papers in the last two years about the existence of a strong association between "bad taste" of butterflies and toughness of wings (DeVries 2002, 2003). One of these papers, "Tough African models and weak mimics: new horizons in the evolution of bad taste," was published in this *Journal* (57: 235-238). Here, I present a critical review of both of DeVries's papers and an opposing point of view.

DeVries postulates that the evolution of "bad taste" (distastefulness) is, in some way, directly connected with the development of tough wings, and that "a toughened wing integument may be a general trait associated with the evolution of distastefulness in butterflies." He argues that toughness of wings appears to be an essential component of butterfly resistance to bird attacks. He claims that he presented experimental proof of his concept of "a wing toughness spectrum that has evolved in parallel with the palatability spectrum" and that "toughness of the wings makes butterflies resistant to handling by predators." I fully disagree with these concepts. I consider them the result of conclusions made on the basis of an experimental design that does not mimic natural conditions.

Under the conditions of the experimental design used by Dr. DeVries, a dead butterfly is firmly "fixed in the grip of a clothing peg with all four wings closed in a natural resting position" leaving free only part of the wings. A clip assembly (the artificial metallic beak) is attached to the hind wings distal margin in such a way that the jaw grips the wings of the dead butterfly between veins Cu1 and 2A. Weight is applied on the artificial beak until there is a tear in the wings and the metallic beak, with the applied weight and the part of the torn wing remaining into its grip, falls into a collecting receptacle. This weight determines the wing tear weight (DeVries 2002, 2003). This weight was found to be in the range of many hundreds of times that of the butterfly tested - 40.0 g for the unpalatable *Amaurus niavius* (a weight that surpasses that of most insectivorous birds), 15g for *Acraea insignis*, and 7.5 g for the palatable *Bicyclus sufitza* and *Junonia terea*.

Under natural conditions the butterfly is not firmly fixed as it is under the conditions of the experimental design used by DeVries. Usually, when caught by a bird, a butterfly hangs freely, with only one wing fixed by the grip of the beak. The body of the live butterfly and the remaining three wings remain free. There is practically no weight applied; the weight of the freely hanging butterfly is negligible. Thus, the force responsible for the tear of the wing under natural conditions is the strength applied by the violent struggling of the freely hanging butterfly to escape from the grip of the beak. Obviously, the stronger the butterfly, the higher is the chance the caught wing will sustain a tear and the butterfly will fly away with only relatively small damage to the wing. If the wing breaks under the weight of the insect, a bird could never catch successfully and consume a butterfly. Thus, under natural conditions, the "wing tear weight" (wtw) is the force applied by the struggling butterfly to free itself from the grip of the beak. It is a very dynamic, pulling, tearing force applied under different conditions than those in the experimental design used. It is not a gradual increase of added weight on the firmly fixed wings of a dead butterfly.

If this force could be measured in grams and approximated that of the weight applied under the conditions of the experiment causing a tear in the wing, the experimental design used by DeVries could reflect natural conditions. DeVries (2002, 2003) claims that "by estimating the force necessary to tear wings" his reports "corroborate the hypothesis that wing toughness may be a corollary of unpalatability in butterflies." However, he does not estimate the force applied on the beak of the bird by the struggling butterfly leading to a tear in the wing at the point where the beak holds the wing. Instead he considers that it is the weight applied on the wing that leads to a tear.

In general, palatable butterflies characteristically have a short, stout fatty body, relatively shorter wings, wide thorax and a fast erratic flight. In contrast, butterflies considered unpalatable are characterized by long slender bodies, elongated wings, narrow thoraxes, fluttering wing beats, and a slow flight in a straight and regular path (Marshall 1909; Chai 1986, 1988; Chai & Srygley 1990; Srygley & Chai 1990; Pinheiro 1996). The flight pattern of palatable butterflies is highly correlated with thoracic muscle mass (Chai & Srygley 1990, Srygley 1994). In fact, most of their wide thoracic cage (85-95% of wet thoracic mass) is filled with massive flight muscles for quick take off, acceleration and increased flight speed (Hocking 1985; Ellington

1991). Evidently, butterflies considered palatable possess a high struggling ability, more strength and thus a better chance to slip out of the beak or escape its grip — leaving the bird with only a small piece of wing in the beak. In contrast, the markedly elongated slender thorax of butterflies considered unpalatable is associated with weaker flight muscles (less muscle mass), which explains their characteristic flight pattern. No doubt, they are less capable of opposing the strong grip of the beak. Evidently, a palatable butterfly, having a low wtw (weaker toughness of the wing), is better protected than a distasteful one from being eaten by a bird by escaping only with a small defect in its wing. Thus, the considered distasteful butterflies, contrary to DeVries's thesis, are less capable of escaping from the grip of the beak, i.e., more vulnerable to predation by birds, despite their higher wtw.

Two questions arise: Why should unpalatable butterflies, despite their supposed strong chemical defense and warning aposematic coloration, evolve wings with a high wtw -- a physical attribute that makes them more vulnerable to predator attack than palatable butterflies which, instead of a chemical defense and warning (aposematic) color patterns for evading a predator, rely on their cryptic color patterns and a fast erratic flight? Why should palatable butterflies with their characteristic fast erratic flight be attacked by birds and comprise their usual diet but unpalatable butterflies, with their characteristically fluttering wing beats, slow flight in a straight and regular path and wings with high wtw, be avoided by predatory birds? It is a paradox that prey that is easy to catch and with a high wtw is avoided and prey that is most difficult to catch and possesses wings with low wtw is preferred by birds and forms part of their regular diet.

I argue that a bird does not reject a butterfly on the basis of aposematic color pattern and a supposed chemical defense, but rather on the basis of a characteristic morphological and behavioral pattern, which provides the bird with a signal whether the prey is actually profitable or unprofitable as a food source (see Kassarov 2003b, c). Only the flight muscles, the reproductive organs, the digestive tract and the abdominal fat have a nutritional value; the remaining chitinous integument, including the wings, is not metabolized. In contrast to the narrow thorax and long slender body of unpalatable butterflies, palatable butterflies characteristically have a wide thorax filled with powerful flight muscles and a stout, fatty abdomen.

It is well known that butterflies considered unpalatable have a tough, very resilient body with a rubbery consistence. Wiklund and Järvi (1982) suggested that, because many aposematic species are tough and difficult to kill (Cott 1940; Edmunds 1974), body toughness (they do not mention the wings) would reduce the risk of a lethal attack and allow them to escape. Birds are very seldom, if at all, able to attack the butterfly's body directly. The relatively small body is well hidden between the large wings and thus protected by them from a direct attack. This fact is especially true for aerial hawkers, the main bird predators of butterflies, who catch their prey on the wing. To reach the body, the bird has to lose energy first to catch the butterfly and then, as most bird species do, dismember the butterfly (another energy and time-consuming process) before finally swallowing it. Whether the body is tough or not tough does not change the fate of the butterfly; a dismembered butterfly is a dead butterfly. If toughness of the integument protects an insect from being eaten by birds, Coleoptera with their "armored" integument should be the best-protected insects. In fact, these insects belong to the regular diet of birds regardless of whether they are hawkers catching their prey on the wing or terrestrial gleaners.

There are no published data concerning a causal relationship between toughness of the integument and chemical compounds that may render the insect distasteful. Such a relationship could exist if based on a chemical reaction; for example, polymerization of the chemical compound responsible for a chemical defense that leads to hardening of the chitinous integument. It seems highly improbable, however, that chemical compounds that supposedly render a butterfly distasteful could cause the integument to become tough and resilient simultaneously (see Kassarov, 2003a).

Thus, how could toughness (high wing tear weight) of the wing be a "corollary of unpalatability" as DeVries (2002, 2003) postulates? It is rather a corollary of palatability. If there is "an evolutionary correlate between toughness of wings and unpalatability," it is logical to expect that there should be an evolutionary corollary between weakness of wings and palatability. Neither is correct. Chemical defense (distastefulness) of the butterfly and toughness of wings are two attributes that evidently do not act in concert but against each other. The weaker the wing (the lower the wtw), the better the chance the butterfly will escape and vice versa - the tougher the wing, the lower the chance that the butterfly will escape. The only way the butterfly can escape is by the wing breaking at the point where the beak holds it. Thus, low wtw facilitates escape. If the wing does not break, the bird will subdue the butterfly, i.e., the butterfly will be a dead butterfly. If taste is the factor responsible for the rejection of a distasteful butterfly by a bird predator, why should nature create conditions for the parallel evolution of a physical attribute (toughness of wing) acting against the supposed chemical defense? The bird's ability to taste a butterfly via beak mark tasting was discussed in detail elsewhere (Kassarov 1999). It was shown that an insectivorous bird is not able to taste a butterfly via beak mark tasting.

There are many more flaws in DeVrises's experimental design. Using only a single size artificial metallic beak (10mm x 3.68mm) makes a reliable comparison of wing tear weights in butterflies with different sizes hardly possible. The smaller the wing the larger will be the torn area of the wing in proportion to its size and the lower will be the wtw; the larger the wing, the smaller will be the torn area and the higher the wtw. The smaller the part of wing gripped by the artificial beak, compared to the remaining free part of the wing, the lower will be the wing tear weight. The closer the artificial beak is placed to the periphery of the distal margin of the wing, the weaker will be the measured toughness of the wing (the wtw). For comparable results, an equal part of the artificial bill should grip the wings of the different butterflies tested (for example, 10.0 mm inward from the outer margin of the wing), and, what is more important, an equal part of the wing of the butterflies with a different size tested should be out of the grip of the clothing peg (only one size clothing peg was used). The greater the part of the wings of the firmly held butterfly (with the wings closed in a natural resting position) secured in the jaws of a wooden clothing peg, the higher will be the wtw. For an assessment of the toughness of the wings of different species belonging to different genera, the artificial beak used in the experiment should grip an equal portion of wing. Whether the artificial beak is placed in the space between two veins or in a space including one or more veins affects markedly the value of the wtw. The "vein tear weight" can be expected to be markedly higher than the wing tear weight measured with the beak placed in the space between two veins. The smaller the wing, the smaller is the space between two veins. Using the same size artificial beak and clothing peg leads inevitably to misleading results. DeVries did not use same sized winged butterflies. Thus, the position of the artificial beak on the wing (angle of attachment, amount of wing gripped, etc.) is most important for receiving comparable results. The presentation of the experimental design in the methods section of DeVries's (2002, 2003) papers is very vague, inviting many questions in regard to its reliability

DeVries (2002, 2003) reports no significant relationship between wing length and wtw among species. This finding is misleading. It does not reflect the conditions observed in nature. As mentioned above, under his experimental design, the artificial beak is anchored in the space between Cu1 and 2A (hind wings) of the firmly fixed four wings in the jaws of a wooden clothing peg. However, under natural conditions, i.e., the butterfly hanging free (not fixed), held only at the point of the grip of the beak, the length of the wing will play a significant role. The strength of the wing will depend on where it is held by the beak. The closer to the apex (away from the base) the weaker the wing. The force applied on the wing by the struggling butterfly increases and the weight of the butterfly also starts to play a role in the process of tearing. I have in my collection of several thousand *Heliconius* (a genus with markedly elongated elegant wings) a great number of specimens with wing damage considered to be the result of a bird attack. Only in a few of them is the damage located in the space between Cu1 and 2A.

Under the conditions of the experiment the strength with which the artificial metal beak holds the wing of each tested dead butterfly remains constant. The initial reaction of the bird to the violent effort of the prey to escape from the grip of the beak is disregarded. If the insect manages to escape, it is usually immediately after being caught — a very dynamic event.

Obviously, if unpalatable butterflies have a high wtw in contrast to the low wtw of the palatable butterflies (DeVries 2002), the supposedly unpalatable models should also have a higher wtw in contrast to that of the palatable mimics. In DeVries (2003), an aposematic model (*Amaurus albimaculata*) was found to have significantly tougher wings than its putative Batesian mimic (*Pseudacreae lucretia*); the mimic was found to have significantly tougher wings than its non-mimic relative, a palatable species belonging to a different genus (*Cymothoe herminia*). Note that the experimental design used to measure the wing tear weights is the same in both papers. No doubt, the results of the experiments performed in both papers will be the same, and the conclusions also. The only difference between the two papers is that *only one* species of unpalatable butterfly considered the model was tested against *only one* species considered a putative mimic (a palatable butterfly) and one non-mimic palatable butterfly (2003), instead of the two palatable and three unpalatable species, again belonging to different genera, but not considered models and mimics (2002).

If mimics have higher wtw than non-mimics, all mimetic butterflies in the genus should have higher wtw than the non-mimics in the same genus. Mean wtw differed significantly among different individuals of the species tested. Figure 1 of DeVries (2002) shows that the highest wtw of *P. lucretia* (N = 23) was far above the lowest wing tear weight of *A. albimaculata*. The same was found for the wing tear weight of *C. herminia* (N = 14) compared to that of *P. lucretia*. Does this marked amplitude between the highest and the lowest wtw in different individuals belonging to the same species indicate differences in toughness of their wings? Different distastefulness? If there is a corollary between wtw and palatability, there should be a significant difference in palatability and flight pattern among individual species (mimetic and non-mimetic) belonging to the same genus. I do not know a butterfly genus comprising species morphologically different or with different flight patterns. Why hould mimetic species have a higher wtw than non-mimetic species belonging to the same or different genera? Is there a corollary between wtw and the ability of a species to mimic a model? Is a certain level of wtw necessary to enable a species to mimic a model?

DeVries states that his method provides a means for asking whether model butterflies are tougher than mimics, and if non-mimic butterflies are the weakest ones. He also states that "by exploring the parallel between the palatability spectrum and wing toughness we may potentially open new horizons in the evolution of bad taste." Obviously, I fully disagree! I consider the results obtained by DeVries (2002, 2003) an experimental artifact. The conclusions drawn are valid only for the conditions of the experiment. They cannot, and should not, be extrapolated to the different conditions existing during an attack of a bird on a butterfly in nature.

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DEFENSIVE FLOCCULENT EMISSIONS IN A TIGER MOTH, *HOMOEOCERA STICTOSOMA* (ARCTIIDAE:ARCTIINAE)

Additional key words: antipredator, Euchromiini, Panama, subabdominal pouch, moth, chemical defense.

Tiger moths (Arctiidae) exhibit a wide range of antipredator adaptations, including ultrasound reception and production, reflex immobilization, wasp mimicry, and chemical secretions in the form of foams and liquids (see Beebe & Kenedy 1957, Blest 1964, Rothschild et al. 1979, Fullard 1990, Conner 1999, Weller et al. 1999). While performing field studies in Panama over the course of several years, we observed what appears to be a novel mode of defense for the Lepidoptera- the expulsion of abdominal 'flocculent' material in a neotropical tiger moth, *Homoeocera stictosoma* Druce (Arctiidae, Arctiinae, Euchromiini) (Jacobson & Weller 2002). In this note we summarize our observations on the behavior associated with flocculent release, and describe some structural and chemical characteristics of the flocculent fibers, and the subabdominal pouches where they are produced and stored.

Certain species of the arctiid tribe Euchromiini possess conspicuous pouches on the ventral anterior abdomen. These pouches have been described only in males to date, and are variously referred to as 'ventral valves' or 'subabdominal pouches' (see Weller et al. 2000). Depending on the species, there may be one or two pouches, which contain either non-deciduous hair pencils or deciduous scales (Weller et al. 2000). The latter, when discharged from the pouch, appear as fluffy white or yellowish cotton, called 'flocculent' by Blest (1964). Despite the widespread occurrence of subabdominal flocculent throughout the Euchromiini (R. Simmons, pers. com.), little is known of its function. Conner et al. (2000) provided experimental evidence for its role in courtship in one species, *Cosmosoma myrodora* Dyar, whereby males increase their probability of mating by enveloping the female with flocculent. Females covered with this material, in turn, are thought to be chemically protected against spiders, due to the high pyrrolizidine alkaloid content of the flocculent filaments. Flocculent has also been documented to play a role in courtship in two other species, *Syntomeida melanthus*, which actively releases flocculent (Sanderford 1992), and *S. ipomoeae*, which flashes its flocculent briefly, but does not release it during courtship (Johnson 2002). In *C. myodora* and other flocculent-bearing species examined, there is no direct evidence that flocculent functions as a mechanism of defense for the possessor, because its production has not been observed to be evoked by handling or other mechanical disturbances of the individual (Blest 1964, Conner et al. 2000, R. Simmons, pers. com,, Yack, pers. obs.). *Homoeocera stictosoma* (Fig. 1) is exceptional in this respect. Blest (1964) commented that this species emits flocculent upon 'light restraint of an individual'. Our observations, outlined below, corroborate Blest's earlier hypothesis.

Moths were collected at ultraviolet and mercury vapor lights in neotropical lowland rainforest on Barro Colorado Island by A. Aiello and R. Silberglied in

FIG. 1. A. A male *Homoeocera stictosoma*, collected on Barro Colorado Island, Panama. B. A male *H. stictosoma* discharging flocculent while being restrained. An arrow points to the subabdominal pouch, where flocculent is rapidly scooped out by the thoracic legs.

March 1980, and by J. Yack in June and October 1998 and September 1999. Moths were collected from sheets and placed in plastic vials where they remained for up to 2 days until being tested. Behavioural observations were made on a total of 9 (3 in 1980; 3 in 1998; 3 in 1999) individuals at the study site, and subsequent anatomical investigations of the subabdominal pouches were carried out on 3 specimens fixed in alcoholic Bouin's (Pantin 1946) or C&C fixative (Chauthani & Callahan 1966), and one dried specimen cleared in warm 10% KOH for 10 minutes. Flocculent material was collected from two live specimens, glued to aluminum stubs and dried overnight. The specimens were coated with gold-palladium for 80 seconds using a Pelco SC-4 Plasma Coater, and examined with an Amray 1810 Scanning Electron Microscope. For chemical analysis, the flocculent was extracted with methanol (2 ml) overnight at room temperature and subsequently analyzed by positive-ion electrospray ionization mass spectroscopy, using a Micromass (Manchester, U.K.) Quattro I mass spectrometer. Moths were identified as male *H. stictosoma* according to their distinctive wing and body markings using Rubio & Pesántez (1997) and Draudt (1915), and through comparison with specimens at the United States National Museum with the assistance of R. Simmons.

Independent behavioral observations were made by one of the authors [AA] in 1980, and another author [JEY] during 1998 and 1999. In 1980, observations on *H. stictosoma* were made while doing palatability experiments with moths on small orb weaver spiders. During these trials, various tiger moth species were tossed from their holding vials into spider webs, and observations were made on the spider's response. To the author's surprise, when a *H. stictosoma* struck the web, it immediately used its legs to pull out abdominal flocculent, and thereby escaped the spider's web, leaving it covered in flocculent. Moths were recaptured and the trials were repeated until the moths ran out of flocculent material. Similar observations were made by J.E.Y. in 1999, whereby a male tossed into a spider web immediately released flocculent and escaped, leaving the web covered with flocculent fibers. In 1998 and 1999, all 6 moths tested discharged flocculent upon being restrained. In no cases was flocculent released while moths were collected or stored in plastic vials, but immediately upon being restrained, all individuals instantaneously responded by releasing clouds of flocculent that surrounded the moth, adhering to the forceps and/or fingers being used to hold the moth (Fig. 1). Flocculent emission discontinued when the moth was placed back in the holding container, but could be provoked repeatedly upon further restraint until the subabdominal pouches were empty.

In *H. stictosoma*, the flocculent fibers are tightly packed inside two subabdominal pouches formed by abdominal sternites I, II, and III (Fig. 2). The largest of the two, the anterior pouch, is covered ventrally by an enlarged sternal plate (SII) that partially overlays the anterior edge of SIII. The opening to the anterior pouch is directed posteriorly. The outermost edge of SII is lined with clear, rounded, non-deciduous scales that may be interpreted as scent scales (cf. Weller et al. 2000). The opening to the smaller posterior pouch occurs between SIII and SIV, with shallow pockets extending both anteriorly and posteriorly. The posterior edge of SIII is also lined with transparent, rectangular scales that are somewhat smaller than those associated with SII. Corresponding to the pattern found in other euchromiines, female *H. stictosoma* lack pouches (R. Simmons, pers. com.). In a detailed examination of the subabdominal pouches in the euchromiine-ctenuchine clade, Weller et al. (2000) described two main types: a single pouch, and a double pouch that corresponds to that of *H. stictosoma*. Species that possess a constricted abdomen (i.e. mimicry of the hymenopteran petiole - wasp mimics) consistently have either a single pouch or no pouch at all, suggesting that there is a trade off between wasp mimicry and the development of subabdominal pouches. *Homoeocera stictosoma*, accordingly, lacks a restricted abdomen.

Although the flocculent fibers are highly compressed within the pouches, when dispersed, they appear as lightweight 'fluff' that floats around the moth. Upon examination with the scanning electron microscope, the flocculent material of *H. stictosoma* is filamentous, composed of flattened, sculptured scales (Fig. 3). Within the Euchromiini, the morphology of flocculent varies considerably, from ribbon like scales to those that resemble twisted chains or even solid cylinders (Sanderford 1992, Boada 1997, Conner et al. 2000). Those described here for *H. stictosoma* appear to be constructed for lightness and strength, and are described as being thin and ribbon like with a network pattern, and covered with a thin translucent film. They most closely resemble the flocculent of *Gymnelia salvini* Butler, *Sarosa* sp., *Myrmecopsis crabonis* Druce, and *Pseudophex polistes* Hubn. (Boada 1997). In *H. stictosoma*, the flocculent also bears a rather strong phenolic odour when released. Mass spectra obtained showed strong ions of m/z 134 and 222, characteristic for a number of pyrrolizidine alkaloids (PAs), therefore suggesting the presence of PAs in the flocculent. The small amounts of flocculent available for analysis however, did not yield enough material for further mass spectroscopic or NMR spectrometric in-

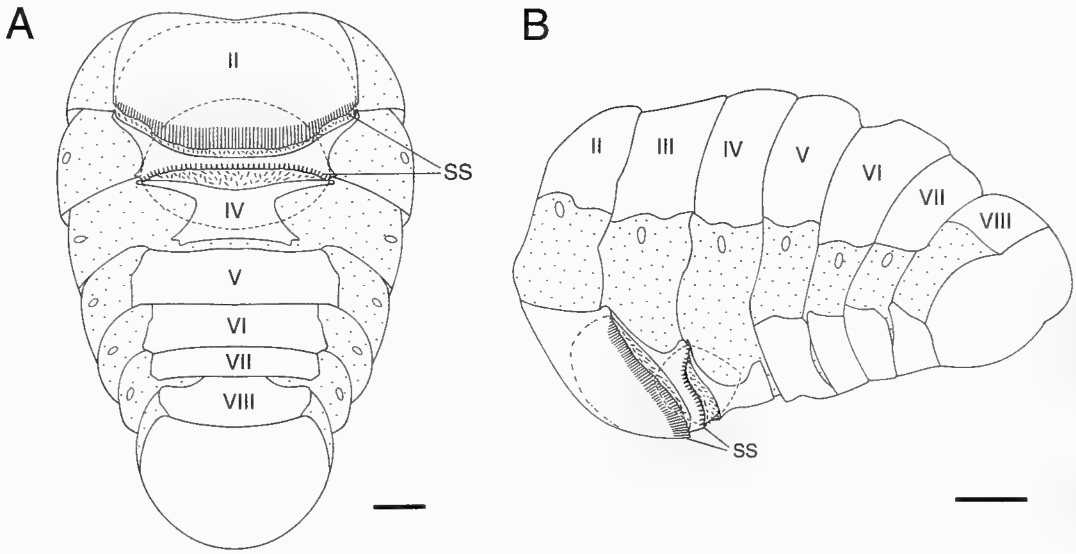

FIG. 2. Schematic representations, based on camera lucida drawings, of the ventral (A) and left lateral (B) views of the abdomen of a male *H. stictosoma*. Flocculent material is densely packed within two subabdominal pouches, the openings of which are depicted by irregularly spaced short lines. Rectangular-shaped scales, interpreted as scent scales (SS) line the edges of the openings to the subabdominal pouches. The larger anterior pouch is defined by sternite II and is directed anteriorly, while the posterior pouch is directed anteriorly and posteriorly. Scale bar: 1 mm.

vestigations to corroborate this hypothesis.

Defensive secretions, including regurgitation, defecation, autohemoraging, and the expulsion of foams and sprays are commonly used among insects (Whitman et al. 1990), but to our knowledge, reflexive discharge of 'scales' has not been documented. Our observations of *H. stictosoma* indicate that flocculent is employed as a defense against spiders and vertebrate predators for the following reasons. 1. Flocculent is consistently discharged upon restraint of an individual. 2. The flocculent scales adhere to the 'attacker' and have a distinct phenolic odour, suggesting a chemical defense. 3. Moths discharge the flocculent when colliding with a spider web, and this is followed by their escape, suggesting that the flocculent coats the web so that the moth does not stick to it. The hypothesis that flocculent functions as an 'instant release' from spider webs and/or an 'anti-consumption' device should be validated experimentally by performing feeding trials with various vertebrate and invertebrate predators, and a detailed analysis of the flocculent chemistry. Also, the role that flocculent plays in the courtship behaviour of *H. stictosoma*, and in the courtship and/or defensive behavior of the other 19 listed *Homoeocera* species (Druce 1881-1900; Draudt 1915) should be explored.

Despite the widespread occurrence of subabdominal pouches in the Euchromiini, little is known of the taxonomic distribution or functional significance of these interesting structures and their constituent flocculent material. To date, the use of flocculent in the context of courtship has been implicated in only 3 species- *C. myrodora* (Conner et al. 2000), *Syntomeida ipomoeae* (Johnson 2002) and *S. melanthus* (Sanderford 1992). In *C. myrodora*, the flocculent may also function indirectly for defense, by protecting the 'adorned' female from spiders (Conner et al. 2000). *Homoeocera stictosoma* is the only species reported to date that unequivocally discharges flocculent upon being restrained. Two other species, *C. teuthras* and *C. myrodora*, have been suggested to use "fluff from the ventral valve" as part of a defensive behavior (Adams 1990), but no other details were provided, and subsequent attempts to induce flocculent production in *C. myrodora* have proved unsuccessful (Conner et al. 2000). It is not possible at this time to know how these various traits evolved, due to our lack of understanding of the functional distribution of flocculent material within the Euchromiini, and the phylogenetic relationships among Euchromiini species. It is interesting to note that some Arctiidae extrude non-deciduous, brightly colored cervical, genital or abdominal hair tufts upon being restrained, and it is believed that the use of these structures in a defensive context de-

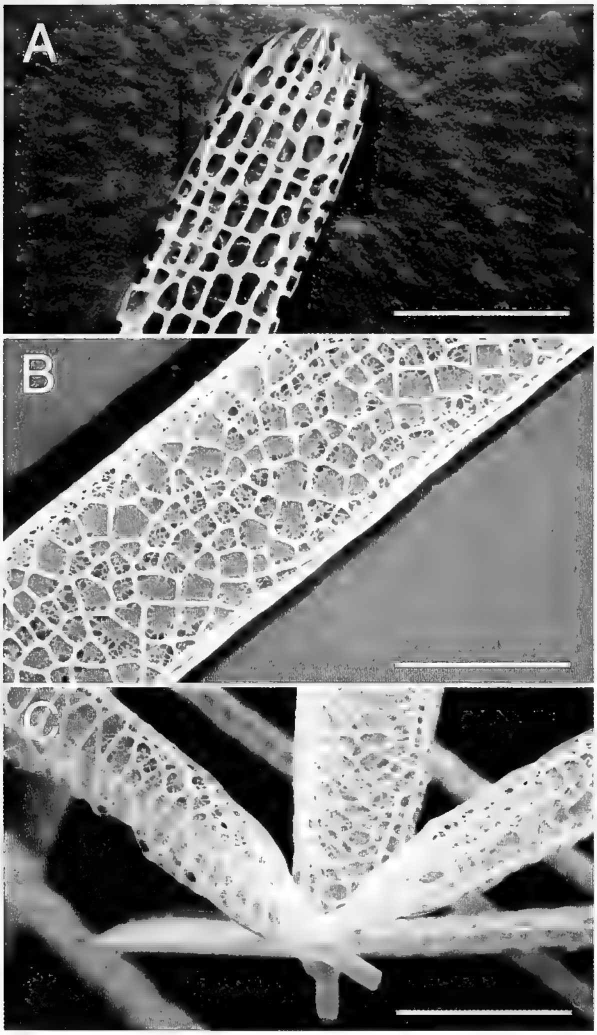

FIG. 3. Filamentous 'scales' from flocculent material in a male *H. stictosoma*. A. Rounded tip of a filament. B. Middle portion of a filament. C. The bases of three filaments where they have broken off of the abdominal pouch. Scale bars: 10 μm.

rives secondarily from a mating function (Blest, 1964). Similarly, one can envision that the defensive emission of flocculent, as we have proposed for *H. stictosoma*, evolved secondarily from a courtship function.

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CATOCYCLOTIS AEMULIUS ADELINA (RIODINIDAE) REVISITED: IT AIN'T NECESSARILY SO

Additional key words: genitalia, allometric changes, Neotropics, Brazil, Costa Rica.

Given their popularity with collectors and entomologists, butterflies are considered one of the taxonomically best-known groups of all insects. Nevertheless, revisiting apparently well known taxa with a modern eye may yield surprises. Consider the case here. The metalmark butterfly currently known as *Catocyclotis aemulius adelina* (Butler, 1872) was originally described in the genus *Lemonias* Hubner, 1907, and considered by Butler (1872) and Godman & Salvin (1879) to be a Central American species closely allied to South American *L. aemulius* (Fabricius, 1793). Subsequently in the influential Genera Insectorum, Stichel (1911) downgraded *adelina* to a subspecies and placed both taxa together under his genus *Catocyclotis* Stichel, 1911, and maintained this arrangement in the Lepidopterorum Catalogus (Stichel 1930-1931). Thus, for over 90 years *adelina* has been regarded as a subspecies of the uncommon, yet broadly distributed species *aemulius*. Nevertheless, to paraphrase the famous song from George Gershwin's folk opera Porgy & Bess, "… the things that you're liable, to read in the Bible, it ain't necessarily so".

During a routine comparative study of male and female genitalia we found conspicuous differences between *C. aemulius adelina* and *C. aemulius aemulius* that correspond with noticeable differences in wing color pattern. These observations suggested that these taxa represent two distinct species, as originally proposed by Butler. The purpose of this study is to reassess the status of taxa currently placed in the genus *Catocyclotis*, provide a diagnosis and illustrations of male and female genitalia of *aemulius* and *adelina*, and point to directions for future research.

Catocyclotis aemulius (Fabricius, 1793)

(Figs. 1-3)

Type species of the genus *Catocyclotis* by original designation (Stichel 1911).

Description: **Male** (Fig. 1) - Dorsal side, FW brown with a single-peaked, pale yellow mark distally on anal edge; brown areas of both FW and HW conspicuously marbled by thin light lines; HW extensively pale yellow (but less so than *adelina*), matching dorsal coloration of abdomen, and bearing marginal spots in cells Rs, M1, M2, Cu1 and Cu2 (not always a full complement of spots is present); abdominal tergites 1-2 brown, 3-8 yellow. Ventral side, HW white and bearing marginal spots as on dorsal side. **Female** (Fig. 1) - wing pattern and color as in male; female abdomen dorsally brown with scattered pale scales that vary in density.

Genitalia: **Male** (Fig. 2) - seventh sternite with thin, elongated rami; aedeagus long with 11 spine-shaped cornuti; uncus with elongated marginal spines (longer than *adelina*); gnathos tip spatulate in ventral view; valva with two defined processes, dorsal process smoothly arched before tip in ventral view (humped in *adelina*), ventral process slightly projected, edge of ventral process with abundant, thickened setae (less abundant and thinner in *adelina*); sclerotized transtilla broader than in *adelina*; saccus tip narrow in ventral view (narrower than *adelina*). **Female** (Fig. 3) - ostium bursa with a sclerotized point that reaches the edge of abdominal segment 8; antrum (defined here as the portion of the ductus bursa posterior to the ductus seminalis) elongated, sclerotized ventrally, wrinkled near ostium bursa, and with an anterior enlargement bearing internal clusters of spines; corpus bursa rounded (even in mated females) with symmetrically positioned signa.

Distribution: Brazil, Ecuador?

Material examined: Milwaukee Public Museum (MPM) - BRAZIL: 1 male, [Santa Catarina] Joinville, 8 June 1955; 1 male, S[anta] Catarina 13 May 1933; 1 male, Rio de Janeiro, Gávea, 21 May 1956; 2 males, Rio [de Janeiro] 20 May 1934; 2 males, 1 dissected, Rio [de Janeiro] 15 May 1941; 1 male, Rio [de Janeiro] 15 May 1941; 1 male, Rio [de Janeiro] 17 June 1931; 1 male, Estado do Rio [de Janeiro], Guapy 29 May 1940; 1 male, [Rio de Janeiro] Colony Guapy 13 May 1964; 1 male, dissected, [Rio de Janeiro] Petrópolis 4 February 1962; 1 male, dissected, Barreira 18 October 1955; 1 male, no data, acquired from P. Gagarin; 1 female, Estado do Rio [de Janeiro] Guapy 13 May 1940; 1 female, Estado do Rio [de Janeiro] Guapy 13 May 1940; 2 females, 1 dissected, [Rio de Janeiro] Mundo Novo 15 May 1940; 1 female, Rio [de Janeiro] Paineira[s] 22 May 1932; 1 female, [Rio de Janeiro] Petrópolis 14 August 1963; 1 female, [Rio de Janeiro] Petrópolis 23 October 1965; 1 female, [Rio de Janeiro] Petrópolis 14 November 1963; 1 female, Rio [de Janeiro] 15 may 1941; 1 female Gávea, Rio [de Janeiro] 15 July 1935. American Museum of Natural History (AMNH) - BRAZIL: 1 male, Rio de Janeiro 4 February [19]66; 1 male, Brazil, Rio [de Janeiro] 18 August [19]11; NO DATA: 1 female.

Biology: Early stage biology unknown. This species is sexually monomorphic, and it inhabits forest areas between sea level (Xerém and Rio de Janeiro, both in Rio de Janeiro state, K. Brown pers. com.) and 900 m (label data above).

Remarks: Stichel (1911) and Seitz (1916) stated that *aemulius* occurred in 'south Brazil' (i.e., Rio de

Janeiro and surrounding areas) while *adelina* was distributed from Costa Rica to Ecuador. Although we did not examine material from Ecuador, the male specimen from Napo illustrated in D'Abrera (1994; note missing abdomen) shows a single-peaked yellow mark distally on the FW anal edge, brown areas of both FW and HW conspicuously marbled by thin light lines, and HW marginal dots - all traits of *aemulius*. Nonetheless, in the D'Abrera (1994) illustration the HW color is orange as in *adelina*. This raises the questions of whether this represents true geographical variation, if the color is a printing artifact, or if the specimen belongs to a different species. Although some of our Brazilian material is old and potentially faded, the AMNH collection includes a male specimen collected by K. S. Brown in Rio de Janeiro in 1966 that is virtually identical in color to a male collected in the same locality in 1911. Therefore, based on D'Abrera (1994) we tentatively expand the previous notion of *aemulius* distribution to include Ecuador, but caution that the constancy of HW color should be verified with more Ecuadorian material.

Catocyclotis adelina (Butler, 1872), revised status

(Figs. 1-3)

Description: **Male** (Fig. 1; color illustration in DeVries 1987, pl. 18) - Dorsal side, FW brown with a double-peaked dark orange mark distally on anal edge; brown areas of FW and HW faintly marbled by thin light lines (conspicuously marbled in *aemulius*), HW not marbled in some specimens; HW extensively orange (more so than *aemulius*), matching dorsal coloration of abdomen, and lacking marginal spots; abdominal tergite 1 brown, 2-8 orange. Ventral side, HW white and normally lacking marginal spots, but in one specimen from Colombia small spots were present in cells M2, Cu1 and Cu2. **Female** (Fig. 1) - wing pattern similar to male, but HW orange color replaced by pale yellow (see DeVries 1987, pl. 18) or nearly white in worn individuals; female abdomen dorsally brown with scattered pale yellow scales that vary in density.

Genitalia: **Male** (Fig. 2) - seventh sternite with short, broad rami; aedeagus short and lacking cornuti; uncus with elongated marginal spines (shorter than *aemulius*); gnathos tip narrow in ventral view; valva with two defined processes, dorsal process humped before tip in ventral view (smoothly arched in *aemulius*), edge of ventral process with thin setae (abundant, thickened in *aemulius*); sclerotized transtilla narrower than in *aemulius*; saccus tip in ventral view broader than *adelina*. **Female** (Fig. 3) - ostium bursa with a sclerotized point that does not reach the edge of abdominal segment 8; antrum (defined here as the portion of the ductus bursa posterior to the ductus seminalis) short, sclerotized ventrally, and broadened near ostium bursa; corpus bursa elongated with asymmetrically positioned signa.

Distribution: Costa Rica, Panama, Colombia.

Material examined: DeVries Collection - COSTA RICA: 1 male, dissected, Puntarenas, Las Alturas 24 May 1991; 1 male, Puntarenas, Las Alturas 25 May 1991; 2 males, Puntarenas, Las Alturas 25 August 1991; 1 male, Moravia de Chirripo 16 April [19]83; 1 female, dissected, [Puntarenas, Las Alturas] site 10C 22 December [19]84. American Museum of Natural History (New York) - COSTA RICA: 1 male, Cairo 27 August [19]31; COLOMBIA: 1 male, S.A., Felipe Ovalle, Q, no date; 1 male, dissected, Amazonas, Rio Cocorna 27 August 1946.

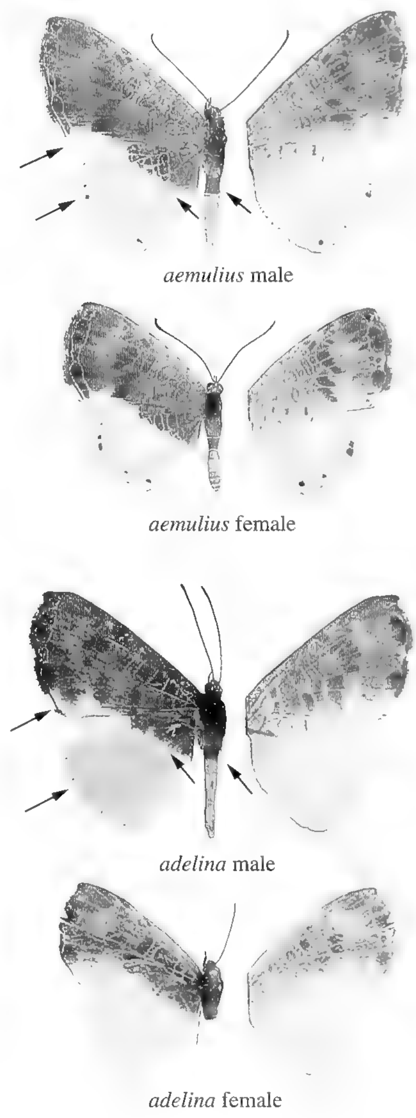

FIG. 1. Male and female habitus of *Catocyclotis aemulius* and *adelina*, dorsal view on the left, ventral on the right. Arrows point to diagnostic characters mentioned in the text. Locality data from top to bottom: *aemulius* male, Brazil (acquired from P. Gagarin); *aemulius* female, Brazil, Rio de Janeiro, Guapy; *adelina* male, Costa Rica, Cairo; *adelina* female, Costa Rica, Puntarenas, Las Alturas.

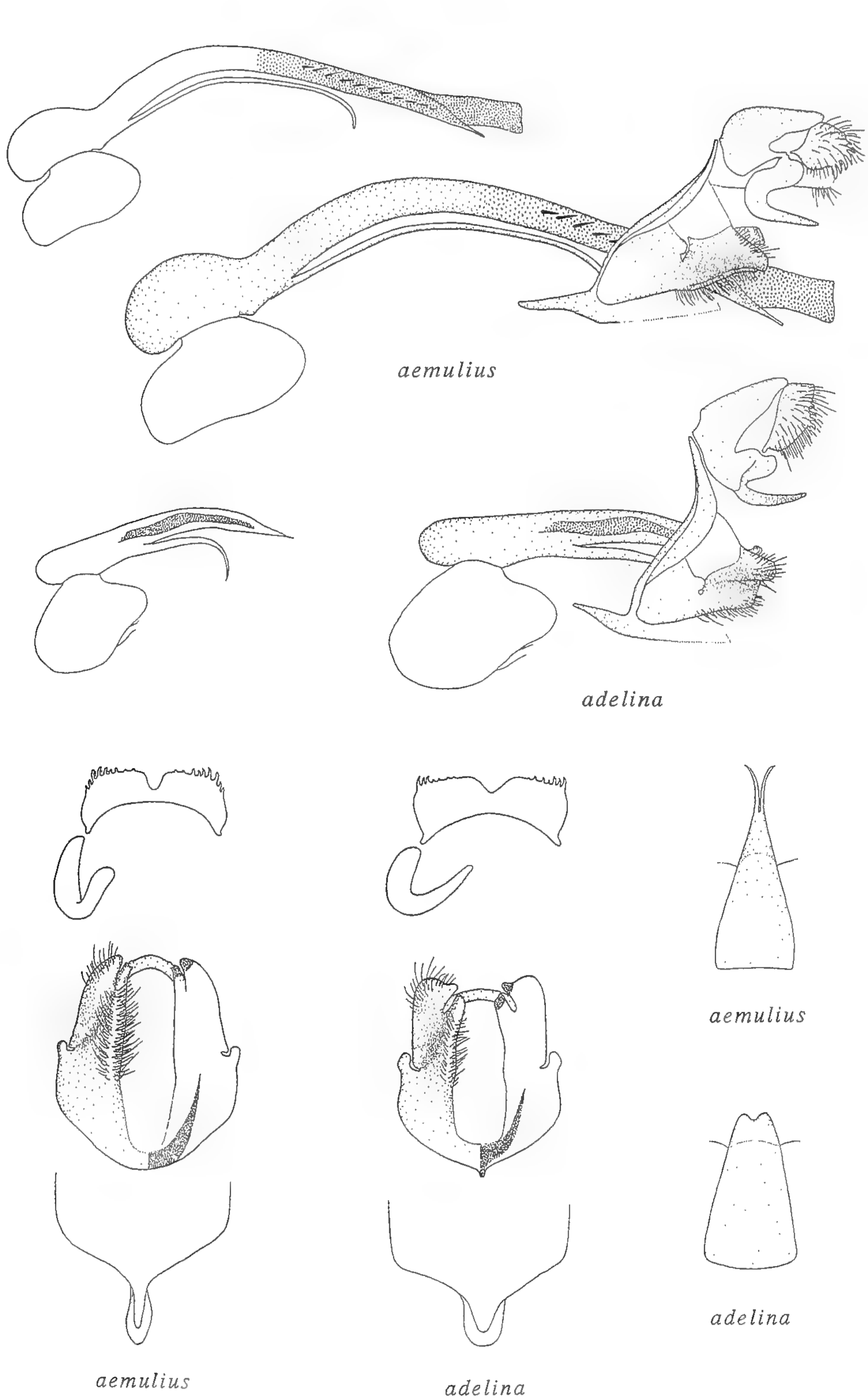

FIG. 2. Male genitalia of *Catocyclotis aemulius* and *adelina*: in lateral view, genitalic capsule and detail of aedeagus; in ventral view, details of the uncus, gnathos, valvae, saccus, and seventh sternite. Valva on the left shows shape and distribution of setae, dense stippling was applied to valva on the right to show areas that are more heavily sclerotized. Locality data: *C. aemulius*, Brazil, Barreira; *C. adelina*, Costa Rica, Puntarenas, Las Alturas.

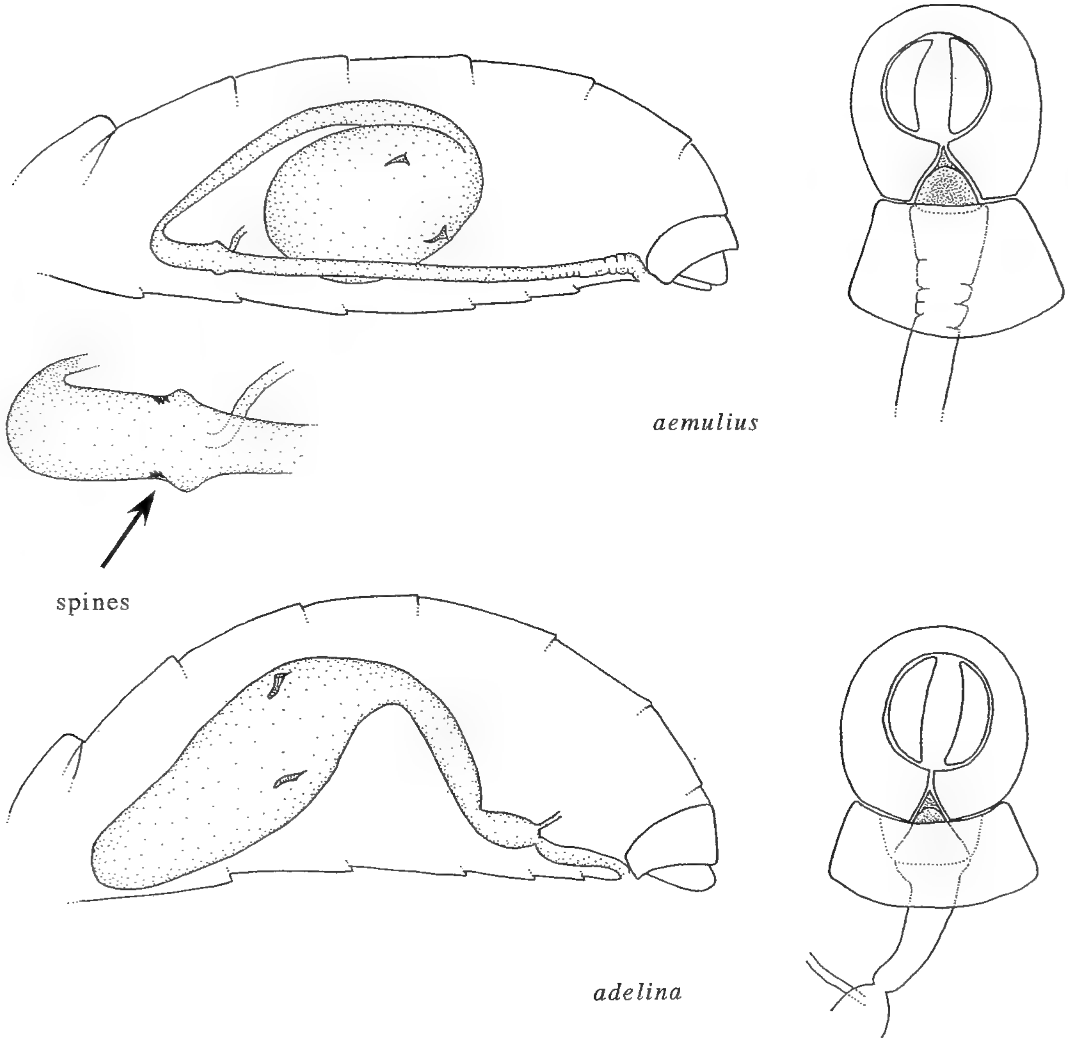

FIG. 3. Female genitalia of *Catocyclotis aemulius* and *adelina*: in lateral view, positioning of antrum+ductus bursa, ductus seminalis, and corpus bursa inside female abdomen, a detail of the ductus bursa of *C. aemulius* shows internal spines, setae show extent of sclerotization, abdomens were dissected open and their outline does not represent actual abdominal width; in ventral view, ostium bursa and seventh sternite, papillae anales are represented schematically. Locality data: *C. aemulius*, Brazil, Rio de Janeiro, Mundo Novo; C. *adelina*, Costa Rica, Puntarenas, Las Alturas.

Biology: This species is reported to occur in forest areas between 800 and 1600 m (DeVries 1987). The sexes are dimorphic. The caterpillar of *C. adelina* and its natural history bear a strong similarity to Nymphidium (e.g., cachrus, hematostictum), and will be described in detail elsewhere (K. Nishida in prep.). The observation that *adelina* produces a clicking sound while in flight (D'Abrera 1994) is of particular interest, and should be verified.

Remarks: The Costa Rican specimen studied by Penz & DeVries (1999) corresponds to *adelina*.

Discussion. Although they have similar wing patterns, differences in wing markings were useful for separating *aemulius* and *adelina*. The shape of the FW anal marking (single- or double-peaked), together with the extent of yellow or orange in the HW plus abdomen, and presence/absence of HW marginal spots, allow species determinations without dissection. These external color pattern characters can be easily used to sort specimens in collections.

The two *Catocyclotis* species studied here showed dramatic differences in male and female genitalia (Fig. 2 and 3). For example, the aedeagus of *aemulius* is much longer than that of *adelina* (Fig. 2), and corresponds to the longer female antrum+ductus bursa in *aemulius* (Fig. 3) - such correspondence has been observed among many other butterfly species (CMP unpublished). Although *aemulius* and *adelina* are closely related, most parts of their genitalia differ, particularly with respect to allometric proportions. These observations suggest to us that when Stichel (1911) considered *adelina* a subspecies of *aemulius*, he did so without comparing their genitalia.

Two lines of inquiry suggest that *Catocyclotis* may include more than two species. Originally Stichel (1911) placed *elpinice* Godman, 1903 in *Catocyclotis*, but subsequently transferred it to his sentiformes section of what is now considered *Adelotypa* (Stichel 1930-31). Of interest is that the specimen of *Adelotypa elpinice* illustrated by D'Abrera (1994) bears strong phenotypic similarities to *C. aemulius* and *adelina*. While not conclusive, such observations indicate that *elpinice* may, upon closer study, be transferred back to Stichel's (1911) home for it in *Catocyclotis*. Secondly, Hall & Harvey (2002) suggested that *Catocyclotis* may include species currently classified in *Mycastor* Callaghan, 1983, but they did not allude to characters or taxa in support of their idea. Based on a cursory comparison of *C. aemulius* and *adelina* with descriptions and illustrations of male genitalia of *Mycastor* by Callaghan (1983) we offer the following observations: (a) *Catocyclotis* and *Mycastor* have a sclerotized transtilla between the valvae - a trait also present in *Nymphidium* (Penz & DeVries 1999 and in prep.); (b) *M. leucarpis* and *Catocyclotis* share a spiny uncus; (c) *M. leucarpis* and *scurrilis* seem to have a valva similar to that of *Catocyclotis*; (d) *M. scurrilis* has a saccus similar to *Catocyclotis*, and the seventh sternite resembles that of *adelina*. These characters lend support to the idea that *Mycastor* includes taxa better placed in *Catocyclotis*. However, it is evident that the total number of species embraced by *Catocyclotis* can only be verified through a comprehensive phylogenetic analysis that includes many Nymphidiini genera and species.

We thank Eric Quinter (American Museum of Natural History) for the loan of specimens under his care, K. Rozema for ideas on riodinid systematics, and anonymous reviewer for suggestions that improved the manuscript. Special thanks to Kenji Nishida for sharing his unpublished information on the biology of C. *adelina*. This study was supported in part by NSF-DEB 03-16505. This paper is dedicated to Adelina "Moreninha" Penz, George Gershwin, and Sportin' Life.

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THE GEOMETRID MOTHS OF EUROPE. VOLUME 4. LARENTIINAE II (PERIZOMINI & EUPITHECIINI) by Vladimir Mironov. Apollo Books, Stenstrup, Denmark. 463 pages, including 16 color plates. Hardback. 2003. ISBN 87-88757-40-4. Price: DKK 720,00.

This is the second volume to appear in a series of six on the geometrid moths of Europe, a series that promises to provide a definitive, copiously illustrated foundation for future studies on the family. This volume is of particular importance as it includes the most diverse but taxonomically most challenging genus in the fauna, *Eupithecia* Curtis. This genus contributes 128 species (out of 1300 worldwide) to the European fauna. These make up about 85% of those treated in the volume, there being five more Eupitheciini and 18 Perizomini.

The author is eminently suited to produce such a work, having worked extensively on the Palaearctic fauna of the group, and provides an essentially eastern perspective, vital when so many of the generic centers of richness of the Palaearctic occur outside Europe. He divides *Eupithecia* into 35 species groups that are defined on genitalia characters.

All the species are illustrated 1.5 times natural size in 16 color plates. Several specimens of each species are illustrated, particularly where variability is encountered, and the text also includes half-tones that indicate key pattern characteristics distinguishing closely related species. The male and female genitalia are also illustrated by line drawings of very high clarity and quality. They have a distinctive style, but a colleague who also works extensively on the group testifies to their accuracy. In many instances the aedeagus vesica is shown everted. These illustrations are numbered with the species number in the main text, which makes it easy for the reader to track a given species through them, the only exceptions being the half-tones and venation diagrams in the body of the text. The distribution of each species is illustrated by a map within or close to the relevant text. This consists of spot localities within a more generally shaded range, though the spots also indicate outlying records.

The text itself is comprehensive, with: synonymy; description of facies and genitalia; details of distribution; phenology and biology, including host-plant records; records of parasitoids; habitat; particular diagnostic features relative to similar species; remarks on taxonomic matters, particularly 25 newly established synonymies.

There is a summary checklist that also notes 53 species from areas adjacent to Europe that potentially could occur there, though these are not illustrated. The reference list is extensive. There is an index to scientific names occurring in the main text, though this does not include synonyms, only taxa recognised at specific or subspecific level, so readers confused as to the fate of taxa newly established as synonyms will need to refer to the Abstract on p. 8. This Abstract also provides a summary of species newly recorded in particular European countries in the main text. The extensive list of Acknowledgements is testimony to the thoroughness and industry on which the volume is based and to the wealth of information resources distilled into it.

One topic where I was hoping for enlightenment but was somewhat disappointed was the treatment of the higher classification. The Larentiinae are the one geometrid group where the greatest species richness and tribal diversity occurs in temperate latitudes. It is from these latitudes, therefore, that clear definition of higher taxa is likely to be established. A treatment in depth of a major component of the larentiine fauna at a continental level might be expected to offer some insight in this area.

Xue & Scoble (2002), investigating the larentiine tribe Asthenini at a global level, found difficulty in distinguishing this tribe from the Eupitheciini, a problem that had previously confronted this reviewer (Holloway, 1997: 120). This book notes in the introduction that the Perizomini are also closely related to the Eupitheciini, and a genus is transferred to the Perizomini as it shows 'all the characteristic morphological features of the tribe'. In the 'Remarks' section of the tribal account, the Perizomini are distinguished from all other geometrids primarily by the presence of labides in the male genitalia. The corresponding account of the Eupitheciini lacks 'Remarks' but notes in the description of the male genitalia that there are labides! Labides are also seen in the Asthenini (Holloway, 1997; Xue & Scoble, 2002: 79-80). The female in Perizomini is distinguished by a heavily sclerotised band arising from spurs from the anterior apophyses and encircling the antrum; this is not present as a complete ring in the Eupitheciini, though the spurs are present. Another feature that appears to distinguish the two tribes is presence in the Eupitheciini of modification to the eighth sternite of the male.

This prompts me to air a more general complaint about sections headed 'Diagnosis' in taxonomic publications. I hope to find highlighted in such sections the diagnostic features that will enable me to distinguish the taxon concerned unambiguously from all others, either individually or in combination. However, I frequently find myself wading through a lengthy general description of features that I suspect are also widely distributed outside the taxon in question, yet are unqualified by diagnostic remarks. In this particular book, the real diagnosis is usually found in the 'Remarks' and 'Similar species' sections and in the text figures; these are of sufficient quality to be truly diagnostic, the features indicated with 'Peterson' pointers, with the excellent illustrations of genitalia in support.

The book is well designed and printed in clear type, and the color values of the plates appear accurate. I can fully recommend it, and expect it to be indispensable in maximising accuracy in future identifications of European Eupitheciini.

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58(3), 2004, 184-185

LAS MARIPOSAS DE MACHU PICCHU. GUÍA ILUSTRADA DE LAS MARIPOSAS DEL SANTUARIO HISTÓRICO MACHU PICCHU, CUZCO, PERÚ, by Gerardo Lamas. Published by the Fondo Nacional para Areas Naturales Protegidas por el Estado (PROFONANPE), Lima, Peru. [iv] + 221 pages, 1 map, 569 color images (34 color plates). Softcover, glossy paper, 21.0 x 29.7 cm, 2003. ISBN 9972-778-10-X. Available for US $25.00 (not including postage), from PROFONANPE, Fondo Nacional para Areas Protegidas por el Estado; Prolongación Arenales 722, Lima-18, Perú. Phone: (511) 212-1010; Fax: (511) 212-1957; e-mail: prf@profonanpe.org.pe; www.profonanpe.org.pe.

Claiming over 3800 species of butterflies, Peru arguably hosts the greatest diversity of butterfly species of any nation on Earth (Lamas 2000). While this new book treats only a small fraction of Peru's species, it treats a fascinating cross-section of Peru's butterfly diversity, of mid- and high-elevation Andean species.

Entirely in Spanish, the twelve-page introduction includes a brief historical review of natural history studies at Machu Picchu, including details of all previous lepidopterological expeditions to the area. A brief description of habitats found at Machu Picchu accompanies notes on butterfly morphology, diversity and biogeography in Cuzco and surrounding Departments. The introduction concludes with information on the book's color illustrations, various sources of related information available on the internet, and acknowledgments.

Following the introduction, 69 pages are dedicated to detailed accounts for 194 genera and 377 butterfly species recorded at Machu Picchu. All taxon names include authorship and date of description, and taxonomy generally follows Lamas (in press). For each included genus, a brief summary of its total diversity and distribution is provided, and in a few cases, references to detailed revisions are included. For each species, notes on identification, distribution, habitats and foodplants at Machu Picchu are provided, along with citations to other publications where taxa have been cited as occurring at Machu Picchu.

The first 6 color plates include 54 images of live butterflies and larvae (of two papilionids), taken in the wild by David H. Ahrenholz. The following 28 color plates include 488 images of pinned specimens, representing all 377 species currently recorded from Machu Picchu. For most species, only one image is provided, though a few species that display strong sexual dimorphism are represented by multiple images. Images are not life size, but each includes a 1 cm scale bar to give an idea of true size.

Following the color plates is a brief two-page bibliography and four appendices. The first appendix is dedicated to descriptions of new taxa. A total of 13 new subspecies are described, in the Pieridae (2), Riodinidae (1), Satyrinae (3), Biblidinae (1), and Ithomiinae (6). The second appendix includes a list of all species recorded at Machu Picchu, indicating the distribution of each at 6 elevational intervals, from 1500 m. to over 4000 m. elevation. The third appendix includes a list of 1373 butterfly taxa currently recorded from the Department of Cuzco, and highlights 278 species that are expected to eventually be found at Machu Picchu. The fourth appendix provides specimen label data for each of the 488 illustrated pinned specimens.

This is perhaps the first book to treat and illustrate the entire known butterfly fauna of any single South American locality. Due to its large size, it is not really a field guide, but nevertheless, this book belongs on the bookshelves of anyone interested in Neotropical butterflies, whether or not they have intentions of traveling to Machu Picchu or elsewhere in Peru. Some of the illustrated taxa are not illustrated elsewhere, and the excellent quality of the illustrations make the book visually quite appealing. Considering its low price, this book is a bargain; the 108 color images of correctly determined skippers, alone, make the book well worth the cost. All information in the book is accurate, the taxonomy and nomenclature is up-to-date (though about mid-2002), and I was unable to find any errors. In conclusion, I strongly recommend this book.

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THE BUTTERFLIES OF ZAMBIA, by Alan Heath, Michael A. Newport & David Hancock. 2002. Published by the African Butterfly Research Institute, Nairobi, Kenya, and The Lepidopterists' Society of Africa. xvii + 137 pages, 3 maps, CD-ROM (PC format) with 2287 color images. Softcover, 20.8 x 29.1 cm, ISBN 0-620-29211-3. Available from The Lepidopterists' Society of Africa for US $50.00, price includes airmail shipping from South Africa. Send book order with shipping address, along with evidence of completed electronic fund transfer (EFT), to Dave L. McDermott, Public Relations Officer, dave@copywise.co.za. Direct EFT of US $50.00 to: NEDBANK, Johannesburg, South Africa, Florida Branch; Branch number 190-541; Account number 1095-032617, indicate "for Zambia book" as reference.

How does a team of authors working with a limited budget go about publishing a tremendous volume of information on 839 species of tropical African butterflies, including multiple color illustrations of virtually every species? The authors of this book found a solution, using a CD-ROM for all illustrations. The book consists of a short introductory text, 137 pages of annotated checklist, a bibliography and index. The CD contains two folders. The "Zambia images" folder includes 2287 color .jpg images of museum specimens of Zambian butterflies, arranged alphabetically. The "Zambia labels" folder contains a .pdf file giving label data for each specimen.

The 17 introductory pages (pp. i-xvii) provide general information on recent books treating the butterfly fauna of other southern African nations, the underlying philosophy of the authors towards the presentation of the book, and a brief explanation of the classification and nomenclature used in the book. Several pages discuss Zambia's topography, climate, 13 major different vegetation types, and a brief political history of the nation. The introduction also includes information on butterfly conservation, the history of butterfly collecting in Zambia, extensive details on the annotated checklist over its 26 year development, a list of the collections consulted, a list of abbreviations used in the checklist that indicate other published sources with illustrations of treated species, and acknowledgments. A brief summary of taxonomic changes made in the annotated checklist is provided, however, discussion of these is provided in the checklist itself. Revised status is proposed for 12 taxa, and one new species of *Charaxes* Ochsenheimer is described by S. F. Henning. The introductory pages conclude with a three-page gazetteer of Zambian localities, and three maps of Zambia.

The 122-page annotated checklist fills the majority of the book, and treats all species recorded from Zambia in detail. A brief summary is given for each family, subfamily and genus that occurs in Zambia, including the authorship for each taxon, and in many cases, brief taxonomic discussions. Below each generic summary, Zambian species and subspecies are listed, again, with authorship indicated for every taxon. Below each listed species or subspecies are abbreviations indicating other works in which that taxon has been illustrated, along with a diagnosis listing important characters for identification. For each taxon, a summary of distributional and phenological data is provided, known foodplants are listed, and for some taxa, a lengthy discussion of variation or taxonomic issues is included. Two pages are dedicated to a discussion of unsubstantiated records. An extensive bibliography of over 100 sources, and 12 pages of index are given at the end of the checklist.

The CD-ROM is in a jacket attached to the inside of the back cover, and can be read only by a PC, not by Macintosh machines. For many species, images of dorsal and ventral surfaces of one specimen are provided, especially when those species display little or no sexual or seasonal variation. For many species, dorsal and ventral surfaces of male and female specimens are illustrated. For some species, seasonal or geographic variation is illustrated in detail, with up to a dozen images. Images are high quality and show well-prepared specimens.

The butterfly images and list of specimen data can be printed, and images can be copied and arranged into plates by the user if so desired, for side-by-side use with the text, away from a computer. I did this, and was able to fit 56 images on each printed page, for a total of 43 color plates. I made a short legend for each plate, placed a printout with the data for the images (as provided on the CD) at the end of my plates, and had them bound together at the corner copy store.

While it did require some time to examine and arrange all the images on the CD, it was a useful crash-course in Zambian butterfly diversity and identification. I quickly learned that there are an amazing number of confusingly similar Zambian species of *Acraea* Fabricius (74 species), *Bicyclus* Kirby (21 species), *Neptis* Fabricius (20 species), *Charaxes* (50 species), *Iolaus* Hübner (32 species), *Deudorix* Hewitson (21 species), *Anthene* Doubleday (23 species) and *Lepidochrysops* Hedicke (28 species). I found few errors in labeling of the images, and a few instances of what appear to be "duplicate" images on the CD; for example the dorsal and ventral images of "male" *Xanthodisca vibius* (Hewitson), *Catopsilia florella* (Fabricius) and *Neocoenyra cooksoni* Druce are actually duplicates of the female images of those species. However, considering the total of 2287 images on the CD, there are remarkably few mistakes, and overall, the library of images on the CD is extraordinarily useful.

This book contains a tremendous wealth of information on the identification, distribution, biology, taxonomy and nomenclature of Zambian butterflies in particular, and of central and southern African butterflies in general. Anyone interested in these subjects will want to own this volume, as will anyone interested in the natural history of southern Africa.

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——— 1961a. Some contributions to population genetics resulting from the study of the Lepidoptera. Adv. Genet. 10:165–216.

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CONTENTS

Papilionoidea of the Evergreen Tropical Forests of Mexico *José L. Salinas-Gutiérrez, Armando Luis-Martínez and Jorge Llorente-Bousquets* ---------- 125

Histoire Générale et Iconographie des Lépidoptères et des Chenilles de l'Amérique Septentrionale by Boisduval & Le Conte (1829-[1837]): Original Drawings used for the Engraved Plates and the True Identities of Four Figured Taxa *John V. Calhoun* ---------- 143

Technical Comment

A critical response to the paper "Tough African models and weak mimics: new horizons in the evolution of bad taste" by P. DeVries published in this journal, vol. 57(3), 2003 *Luka Kassarov* ---------- 169

General Notes

Defensive Flocculent Emissions in a Tiger Moth, *Homoeocera Stictosoma* (Arctiidae:Arctiinae) *Jayne E. Yack, Tiffany A. Timbers, William E. Conner, Annette Aiello and Frank C. Schroeder* ---------- 173

Catocyclotis Aemulius Adelina (Riodinidae) Revisited: it Ain't Necessarily so *Carla Penz and Phil DeVries* ---------- 178

Book Reviews

The Geometrid Moths of Europe. Volume 4. Larentiinae II (Perizomini & Eupitheciini) *Jeremy D. Holloway* ---------- 183

Las Mariposas de Machu Picchu. Guía ilustrada de las Mariposas del Santuari Histórico Machu Picchu, Cuzco, Perú *Andrew D. Warren* ---------- 184

The Butterflies of Zambia *Andrew D. Warren* ---------- 185

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